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A spatially integrated framework for assessing socio-ecological drivers of carnivore decline

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Summary

1. Habitat loss, fragmentation and degradation are key threats to the long-term persistence of carnivores, which are also susceptible to direct persecution by people. Integrating natural and social science methods to examine how habitat configuration/quality and human-predator relations may interact in space and time to effect carnivore populations existing within human-dominated landscapes will help prioritise conservation investment and action effectively.
2. We propose a socio-ecological modelling framework to evaluate drivers of carnivore decline in landscapes where predators and people coexist. By collecting social and ecological data at the same spatial scale, candidate models can be used to quantify and tease apart the relative importance of different threats.
3. We apply our methodological framework to an empirical case study, the threatened guiña (*Leopardus guigna*) in the temperate forest ecoregion of southern Chile, to illustrate its use. The existing literature suggests that the species is declining due to habitat loss, fragmentation and persecution in response to livestock predation. Data used in modelling were derived from four seasons of camera-trap surveys, remote-sensed images and household questionnaires.
4. Occupancy dynamics were explained by habitat configuration/quality covariates rather than by human-predator relations. Guiñas can tolerate a high degree of habitat loss (>80% within a home range). They are primarily impacted by fragmentation and land subdivision (larger farms being divided into smaller ones). Ten percent of surveyed farmers (N=233) reported illegally killing the species over the past decade.
5. *Synthesis and applications*. By integrating ecological and social data into a single modelling framework, our study demonstrates the value of an interdisciplinary approach to assessing the potential threats to a carnivore. It has allowed us to tease apart effectively the relative importance of different potential extinction pressures, make informed conservation recommendations and prioritise where future interventions should be targeted. Specifically for the guiña, we have identified that human-dominated landscapes with large intensive farms can be of conservation value, as long as an appropriate network of habitat patches are maintained

within the matrix. Conservation efforts to secure the long-term persistence of the species should focus on reducing habitat fragmentation, rather than human persecution in our study system.

Key-words: camera-trapping, conservation, randomised response technique, habitat fragmentation, habitat loss, human-predator relations, human-wildlife co-existence, illegal killing, *Leopardus guigna*, multi-season occupancy modelling

Introduction

Land-use change is one of the greatest threats facing terrestrial biodiversity globally (Sala *et al.* 2000), as species persistence is negatively influenced by habitat loss, fragmentation, degradation and isolation (Henle *et al.* 2004a). In general, species characterised by a low reproductive rate, low population density, large individual area requirements or a narrow niche are more sensitive to habitat loss and fragmentation (Fahrig 2002; Henle *et al.* 2004b) and, therefore, have a higher risk of extinction (Purvis *et al.* 2000). Consequently, many territorial carnivores are particularly vulnerable to land-use change. Furthermore, the disappearance of such apex predators from ecosystems can have substantial cascading impacts on other species (Estes *et al.* 2011; Ripple *et al.* 2014).

Additionally, in human-dominated landscapes, mammal populations are threatened directly by the behaviour of people (Ceballos *et al.* 2005). For instance, larger species (body mass >1 kg) are often persecuted because they are considered a pest, food source or marketable commodity (Woodroffe, Thirgood & Rabinowitz 2005). Carnivores are especially vulnerable to persecution after livestock predation, attacks on humans, or as a result of deep rooted social norms or cultural practices (Treves & Karanth 2003; Inskip & Zimmermann 2009; Marchini & Macdonald 2012). Indirectly, many mammals are also threatened by factors such as the introduction of invasive plant species, which reduce habitat complexity (Rojas *et al.* 2011), and domestic pets, which can transmit diseases or compete for resources (Hughes & Macdonald 2013).

To ensure the long-term future of carnivore populations within human-dominated landscapes outside protected areas, it is imperative that we identify potential ecological and social drivers of species decline and assess their relative importance (Redpath *et al.* 2013). For example, it is essential to disentangle the impacts of habitat loss and fragmentation on a species, as the interventions required to alleviate the pressures associated with the two processes are likely to be different (Fahrig 2003; Fischer & Lindenmayer 2007). If habitat loss is the dominant issue causing population reduction, then large patches may need to be protected to ensure long-term survival, whereas a certain configuration of remnant vegetation may be required if fragmentation is the main threat. At the same time, it is important to understand if, how and why people persecute species, if conservationists are to facilitate human-wildlife coexistence (St John, Keane & Milner-Gulland 2013). However, there is a paucity of interdisciplinary research that evaluates explicitly both ecological and social drivers of species decline in a single coherent framework, across geographic scales pertinent to informing conservation decision-making (Dickman 2010).

From an ecological perspective, data derived from camera-traps and analysed via occupancy models are widely used to study carnivores over large geographic areas (Burton *et al.* 2015; Steenweg *et al.* 2016). Occupancy modelling offers a flexible framework that can account for imperfect detection and missing observations, making it highly applicable to elusive mammals of conservation concern (MacKenzie *et al.* 2003; MacKenzie & Reardon 2013). Monitoring population dynamics temporally, and identifying the factors linked to any decline, is critical for management (Di Fonzo et al. 2016). For this reason, dynamic (i.e. multi-season) occupancy models are particularly useful because they examine trends through time and can be used to ascertain the drivers underlying observed changes in occupancy (MacKenzie *et al.* 2003, 2006). Similarly, there are a range of specialised social science methods for asking sensitive questions that can be used to yield valuable information on human behaviour, including the illegal killing of species (Nuno & St. John 2015). One such example is the unmatched count technique, which has recently been used to examine the spatial distribution of hunting and its proximity to Serengeti National Park, Tanzania (Nuno *et al.* 2013), and bird hunting in Portugal (Fairbrass *et al.* 2016). Another method is the randomised response technique (RRT),

previously used to estimate the prevalence of predator persecution in South Africa (St John *et al.* 2012) and vulture poisoning in Namibia (Santangeli *et al.* 2016).

In this paper, we propose an integrated socio-ecological modelling framework that draws together these natural and social science methods to examine how habitat configuration/quality and "human-predator relations" (Pooley *et al.* 2016) may interact in space and time to effect carnivore populations across a human-dominated landscape. An important aspect of the approach is that the social and ecological data are collected at a matched spatial scale, allowing different potential drivers of decline to be contrasted and evaluated. We showcase the approach using the guiña (*Leopardus guigna*), a felid listed as Vulnerable on the International Union for Conservation of Nature (IUCN) Red List, as a case study species. Specifically, we use data derived from multi-season camera-trap surveys, remote-sensed images and a household questionnaire which uses RRT to estimate prevalence and predictors of illegal killing. The outputs from our framework provide a robust evidence-base to direct future conservation investment and efforts.

Methods

Integrated socio-ecological framework

Our proposed framework comprises four stages (Fig. 1). The first step is to gather information on the ecology of the species and likely drivers of decline, including habitat configuration/quality issues (e.g. habitat loss, habitat fragmentation, presence/absence of habitat requirements) and human-predator relations (e.g. species encounter frequency, livestock predation experiences), that require evaluation. The best available information can be acquired from sources such as peer-reviewed and grey literature, experts and IUCN Red List assessments. The next task, step two, is to define a suite of candidate models *a priori* to assess and quantify the potential social and ecological predictors on species occupancy dynamics. Dynamic occupancy models estimate parameters of change across a landscape, including the probability of a sample unit (SU) becoming occupied (local colonisation) or unoccupied (local extinction) over time (MacKenzie *et al.* 2006).

The third step involves the collection of ecological and social data in SUs distributed across the landscape, to parametise the models. Camera-trap survey effort allocation (i.e. the number of SUs that need to be surveyed) for occupancy estimation can be determined *a priori* using freely-available tools (Gálvez *et al.* 2016). The final stage is the evaluation of evidence, using standard model selection methods (Burnham & Anderson 2002) to establish which of the social and ecological variables within the candidate models are indeed important predictors of occupancy, and to contrast their relative importance. Results from the models can be contextualised with additional supporting evidence not embedded in the models to inform where conservation action should be directed. For instance, during questionnaire delivery, valuable qualitative data may be recorded that provides in-depth insights related to the human-predator system (e.g. Inskip *et al.* 2014).

Study species and system

The guiña is the smallest neotropical felid (<2 kg) (Napolitano *et al.* 2015). It is thought to require forest habitat with dense understory and the presence of bamboo (*Chusquea* spp.) (Nowell & Jackson 1996; Dunstone *et al.* 2002), but is also known to occupy remnant forest patches within agricultural areas (Sanderson, Sunquist & Iriarte 2002; Acosta-Jamett & Simonetti 2004; Gálvez *et al.* 2013; Fleschutz *et al.* 2016; Schüttler *et al.* 2017). Guiñas are considered pests by some people as they can predate chickens and, while the extent of persecution has not been formally assessed, killings have been reported (Sanderson, Sunquist & Iriarte 2002; Gálvez *et al.* 2013). Killing predominately occurs when the felid enters a chicken coop (Gálvez & Bonacic 2008). Due to these attributes, the species makes an ideal case study to explore how habitat configuration/quality and human-predator relations may interact in space and time to influence the population dynamics of a threatened carnivore existing in a human-dominated landscape.

The study was conducted in the Araucanía region in southern Chile (Fig. 2), at the northern limit of the South American temperate forest eco-region (39º15´S, 71º48´W) (Armesto *et al.* 1998). The system comprises two distinct geographical sections common throughout Southern Chile: the Andes mountain range and central valley. Land-use in the latter is primarily intensive agriculture (e.g.

cereals, livestock, fruit trees) and urban settlements, whereas farmland in the Andes (occurring <600 m.a.s.l) is less intensively used and surrounded by tracks of continuous forest on steep slopes and protected areas (>800 m.a.s.l). The natural vegetation across the study landscape consists of deciduous and evergreen *Nothofagus* forest (Luebert & Pliscoff 2006), which remains as a patchy mosaic in agricultural valleys and as continuous tracts at higher elevations within the mountains (Miranda *et al.* 2015).

Data collection

Predator detection/non-detection data

We obtained predator detection/non-detection data via a camera-trap survey. Potential SUs were defined by laying a grid of 4 km^2 across the study region, representing a gradient of forest habitat fragmentation due to agricultural use and human settlement below 600 m.a.s.l. The size of the SUs was informed by mean observed guiña home range size estimates of collared individuals in the study area (MCP 95% mean=270 ±137 ha; Schüttler *et al.* 2017).

In this study system, detectability was modelled based on the assumption that a two-day survey block is a separate independent sampling occasion. This time threshold was chosen because initial observations of collared individuals indicated that they did not stay longer than this time in any single location (Schüttler et al. unpublished data). Minimum survey effort requirements (i.e. number of SUs and sampling occasions) were determined following Guillera-Arroita, Ridout & Morgan (2010), using species specific parameter values from Gálvez *et al.* (2013) and a target statistical precision in occupancy estimation of SE<0.075. A total of 145 SUs were selected at random from the grid of 230 cells, with 73 and 72 located in the central valley and Andes mountain valley respectively (Fig. 2). The Andean valleys were surveyed for four seasons (summer 2012, summer 2013, spring 2013, summer 2014), while the central valley was surveyed for the latter three seasons. A total of four rotations (i.e. blocks of camera-traps) were used to survey all SUs within a 100-day period each season. Detection/non-detection data were thus collected for 20-24 days per SU, resulting in 10-12 sampling occasions per SU. Two camera-traps (Bushnell ™trophy cam 2012) were used per SU,

positioned 100-700 m apart, with a minimum distance of >2 km between camera-traps in adjacent SUs. The detection histories of both camera-traps in a SU were pooled, and camera-trap malfunctions or thefts (five in total) were treated as missing observations.

Habitat configuration/quality data

The extent of habitat loss and fragmentation were evaluated using ecologically meaningful metrics which have been reported in the literature as being relevant to guiñas, using either field or remote-sensed landcover data (Table 1, Appendix S1 & Table S1). The metrics were measured within a 300 ha circular buffer, centred on the midpoint between both cameras in each SU using FRAGSTATS 4.1 (McGarigal *et al.* 2002). Habitat quality surrounding a camera-trap might influence species activity (Acosta-Jamett, Simonetti, 2004). We collected data on a number of variables within a 25-m radius around each camera-trap (Table S1), as this is deemed to be the area over which localised conditions may influence species detectability. The habitat quality data from both camera-traps in each SU were pooled and the median was used if values differed.

Human-predator relations data

Between May and September 2013 the questionnaire (Appendix S2) was administered face-to-face by NG who is Chilean and had no previous interaction with respondents. All SUs contained residential properties and one or two households closest to the camera-trap locations were surveyed (mean number of households per km^2 across the study landscape: 3.4; range: 1.4 to 5.1 from INE 2002). For each household, the family member deemed to be most knowledgeable with respect to farm management and decision-making was surveyed. The questionnaire gathered data on socio-demographic/economic background, guiña encounters, livestock ownership, frequency of livestock predation by guiñas and ownership of dogs on the land parcel. To measure tolerance to livestock predation, participants were asked how they would respond to different scenarios of livestock loss (mortality of 2, 10, 25, 50, >50 animals), with one possible option explicitly stating that they would kill guiña. These data were also used as predictors of killing behaviour in the RRT analysis (see

222 below). The questionnaire was piloted with 10 local householders living outside the SUs; their
223 feedback was used to improve the wording, order and time scale of predation and encounter questions.
224
225 The potential occupancy model predictors (Tables 1 & S1, Appendix S2) were calculated per SU.
226 Where questionnaire responses differed within a SU (e.g. one household report predation and the
227 other did not), presence of the event (e.g. predation) was used as a covariate for that particular SU.
228 For all quantitative measures, and when both respondents report the event (e.g. frequency of
229 predation) median values were used.
230
231 *Illegal killing prevalence across the landscape (other evidence)*
232 As it is illegal to kill guiñas in Chile (Law 19.473 Ministry of Agriculture), RRT (Nuno & St. John
233 2015) was used to ask this sensitive question as part of the questionnaire (Appendix S2). Since RRT,
234 like other methods for asking sensitive questions, require a large sample size for precise estimation of
235 behaviour prevalence (Nuno & St. John 2015), we pooled RRT data from all participants to estimate
236 the prevalence of illegal guiña killing across the landscape over the past decade. We explored
237 predictors that might explain this human behaviour (St John *et al.* 2012).
238
239 RRT data were bootstrapped 1000 times to obtain a 95% confidence interval. We tested seven non-
240 correlated predictors of illegal guiña killing: age, income, frequency of guiña encounters, number of
241 chickens owned (all continuous variables standardized to z-scores), economic dependency on their
242 land parcel (1=no dependency; 2=partially dependency; 3=complete dependency), knowledge of the
243 guiña's legal protection status (0=hunting prohibited; 1=do not know; 2=hunting permitted), and
244 intention to kill a guiña under a hypothetical predation scenario (0=do nothing; 1=manage guiña;
245 2=kill guiña) (Appendix S2). We used R (version 3.2.3; R Core Team, 2014) to run the RRlog
246 function of the package RRreg (version 0.5.0; Heck & Moshagen 2016) to conduct a multivariate
247 logistic regression using the model for 'forced response' RRT data. We fitted a logistic regression
248 model with the potential predictors of killing behaviour and evaluated their significance with

likelihood ratio tests (LRT ΔG^2). Odds ratios and their confidence values are presented for model covariates.

Integrated socio-ecological modelling

First, we evaluated the existence of spatial autocorrelation with detection/non-detection data for each SU, using Moran's *I* index based on similarity between points (Dormann *et al.* 2007). We used a fixed band distance of 3 km from the midpoint of camera-traps, equating to an area three times larger than a guiña home range.

We fitted models of occupancy dynamics (MacKenzie *et al.* 2003) using PRESENCE, which obtains maximum-likelihood estimates via numerical optimisation (Hines 2006). The probabilities of initial occupancy (ψ), colonisation (γ), local extinction (ε) and detection sites (p) were used as model parameters. We conducted a preliminary investigation to assess whether a base model structure with Markovian dependence was more appropriate for describing seasonal dynamics, rather than assuming no occupancy changes occur or that changes happen at random (MacKenzie *et al.* 2006). Once the best model structure had been determined, we then fitted models with habitat configuration/quality and human-predator predictors.

A total of 15 potential model predictors were tested for collinearity and, in instances where variables were correlated (Pearson's/Spearman's $|r|>0.7$), we retained the covariate that conferred greater ecological/social meaning and ease of interpretation (Tables 1 & S1). All continuous variables, except percentages, were standardized to z-scores. We approached model selection by increasing model complexity gradually, fitting predictors for each model parameter separately and assessing model performance using Akaike's Information Criterion (AIC). Models that were within <2 ΔAIC were considered to have substantial support (Burnham & Anderson 2002), and thus these predictors were selected and used in the next step in a forward manner (e.g. Kéry, Guillera-Arroita & Lahoz-Monfort 2013). To prevent over fitting (Burnham & Anderson 2002), we kept models with only one predictor

per parameter, with the exception of one model which evaluated the additive effect of shrub and forest cover (shrub is a marginal habitat for the study species; Dunstone *et al.* 2002).

A set of detection models were fitted using the best base structure. Subsequently, we evaluated models that included habitat configuration/quality and human-predator relations data to test its effect on initial occupancy (ψ_1), while keeping colonisation and extinction specific. The best initial occupancy and detection models were then used to add further complexity to the colonisation and extinction components. We fitted all predictors for extinction. However, we assume that colonisation between seasons is primarily influenced by habitat configuration/quality variables, rather than human-predator relations. To explore the candidate model space, we worked on the structure for extinction probability followed by colonisation, and then repeated the process vice versa (Kéry, Guillera□Arroita & Lahoz□Monfort 2013). A constant or null model was included in all candidate model sets. Models with convergence problems or implausible parameter estimates (i.e. very large estimates and standard errors) were eliminated from each set.

Goodness of fit was evaluated by bootstrapping 5000 iterations (MacKenzie and Bailey 2004) in the R package AICcmodavg. This test provides a model fit statistic based on consideration of the data from all seasons at once (*P*-Global), as well as separate statistics for each season. We used the predict function in R package unmarked (Fiske & Chandler 2011) to produce plots of estimated relationships with the predictors and derive estimates of occupancy for each of the seasons.

All aspects of this project were approved by the School of Anthropology and Conservation Research and Research Ethics Committee, University of Kent, as well as the Villarrica Campus Committee of the Pontificia Universidad Católica de Chile.

Results

Habitat configuration/quality data

303 Across the landscape, variation in the degree of habitat loss and fragmentation was substantial. Forest
304 cover in SU's ranged from 1.8-76% (mean=27.5%; SD=18.9), and shrub cover followed a similar
305 pattern (range: 9.1-53.1%; mean=26%; SD=8.3). The number of habitat patches per SU varied
306 between 14 and 163 (mean=52.9; SD=25.7), and patch shape was diverse (index range: 1.3 (highly
307 irregular forms) to 7.8 (regular forms); mean=3.13; SD=1.3). Some SUs included a relatively high
308 length of edge (~48,000 m), whereas others had as little as 4,755 m.
309
310 ***Human-predator relations data and illegal killing prevalence across the landscape***
311 A total of 233 respondents completed the questionnaire, of which 20% were women and 80% men.
312 The median age of respondents was 55 years (interquartile range: 46-67). Participants had lived in
313 their properties for 25-50 years (median=35), which varied from 1-1,200 ha in size (median=29).
314 Land subdivision within SUs also varied widely (range: 1-314 properties; mean=41.3; SD=37.2).
315 Respondents, on average, received a monthly income equivalent to US$558 (SD=2.81) and had
316 completed 10 years of formal schooling.
317
318 Encounters with guiñas were rare. Nearly half of the respondents (49%, n=116) reported seeing a
319 guiña during their lifetime. However, on average, the sighting occurred 17 years ago (SD=15). This
320 percentage dropped to 10% and 21% during the last four (within the timeframe of the camera-trap
321 survey) and 10 years (time period for the RRT question) respectively. Predation events were also
322 uncommon. Only 16% of respondents (n=37) attributed a livestock predation event in their lifetime to
323 a guiña, with just 7% (n=16) stating that this had occurred in the past decade. Of the guiña predation
324 events over the past decade (n=16), 81% were recorded in Andean SUs.
325
326 When presented with scenario-style questions concerning hypothetical livestock predation by a guiña,
327 38% (n=89) of respondents stated that they would kill the felid if two chickens were lost, rising to
328 60% (n=140) if 25 chickens were attacked. Using RRT, we found that 10% of respondents admitted to
329 having killed a guiña in the last 10 years (SE=0.09; 95% CI=0.02-0.18). The likelihood of a
330 respondent admitting to killing guiña increased significantly with encounter frequency (β=0.85,

SE=0.50; LRT ΔG^2 =4.18, p=0.04); those reporting the highest level of encounter rate were 2.3 times more likely to have killed the species compared to those not encountering guiña (Table 2). Data from the scenario-based question on predation were excluded from the model due to a high β and associated standard error.

Detection/non-detection data

A total of 23,373 camera-trap days returned 713 sampling occasions with a guiña detection (season 1=96; season 2=185; season 3=240; season 4=192). The naïve occupancy (i.e. proportion of sites with detection) was similar across all four seasons (0.54; 0.52; 0.58; 0.59) and between the central valley and Andean SUs (both areas >0.5). There was no evidence of spatial autocorrelation among SUs during any survey season (season 1 Moran's I=-0.03 (α=0.74); season 2 I=0.05 (α=0.31); season 3 I=0.05 (α=0.36); season 4 I=0.07 (α=0.17)).

Integrated socio-ecological multi-season occupancy modelling

Our preliminary evaluation indicated that a Markovian dependence model structure was an appropriate description of the data. This dependence implies that guiña presence at a given site in a particular season is dependent on whether that site was occupied in the previous season (Table 3). Model 1.1 was chosen as the base structure for the modelling procedure because: (i) it is supported by AIC; and, (ii) its parameterisation using extinction and colonisation (i.e. not derived parameters) allowed the role of different potential predictors to be tested on these population processes. Also, letting extinction and colonisation be season-specific accommodated for unequal time intervals between sampling seasons.

Model selection for detection (models 2.1-2.7; Table 4) revealed a positive relationship with understory vegetation cover (β_1=0.343; SE=0.055; Fig. 3b). There was no evidence of an effect associated with the rotational camera-trap survey design, and none of the other predictors were substantiated. Forest cover best explained initial occupancy (models 3.0-3.6; Table 4), with initial occupancy being higher in sites with less forest cover, although the estimated relationship was weak

(β_1 =-0.0363; SE=0.0138; Fig. 3a). Adding shrub cover only improved model fit marginally. Fragmentation metrics and land subdivision were not supported as good predictors.

Model selection for extinction and colonisation (models 4.0-4.18 and 5.0-5.12; Table 4) reflected the same trends, irrespective of the order in which parameters were considered. Extinction, rather than colonisation, yielded predictors that improved model fit compared to the null model. Where predictors were fitted first on colonisation (models 5.0-5.5), none of the models tested improved fit substantially compared to the null model. This indicated that, of the available predictors, colonisation was only explained by seasonal differences. The human-predator predictors were not supported as drivers of either initial occupancy or extinction probability (Table 4).

We fitted a final model (model 5.6; Table 4) with number of patches and land subdivision, which were identified as important predictors in the two top competing extinction models (models 5.7 and 5.8). This model was well supported. A goodness-of-fit test suggested lack of fit based on the global metric (*P*-global<0.05), but inspection of survey-specific results show no such evidence (p>0.05) apart from season 2 (p=0.032). Inspecting the season 2 data, we found that the relatively large statistic value appeared to be driven by just a few sites with unlikely capture histories (i.e. <12 detections). Given this, and the fact that data from the other seasons do not show lack of fit, we deem that the final model explains the data appropriately. The model predicts that SU extinction probability becomes high (>0.6) when there are less than 27 habitat patches, and more than 116 land subdivisions (β_1=-0.900; SE=0.451 and β_1=0.944; SE=0.373 respectively; Figs. 3cd). Occupancy estimates were high across seasons with derived seasonal estimates of 0.78 (SE=0.09), 0.64 (SE=0.06), 0.80 (SE=0.06) and 0.83 (SE=0.06).

Discussion

The integrated socio-ecological modelling framework we present here provides important insights into how habitat configuration/quality and human-predator relations may interact in space and time to effect carnivore populations existing across a human-dominated landscape. We were able to

disentangle the relative impact of a range of threats that have been highlighted previously in the literature as potential drivers of decline for our case study species the guiña.

The guiña is an elusive forest specialist. As such, one might predict that the species would be highly susceptible to both habitat loss and fragmentation (Henle *et al.* 2004b; Ewers & Didham 2006). While the relationship between occupancy and higher levels of forest cover (Fig. 3a) does suggest guiñas are likely to occupy areas with a large spatial extent of available habitat, our results also indicate that the species can tolerate extensive habitat loss. The effects of habitat loss could be confounded by time, and it is possible that we are not yet observing the impacts of this ecological process (Ewers & Didham 2006). However, this is unlikely to be the case in this landscape as over 67% of the original forest cover was lost by 1970 and, since then, deforestation rates have been low (Miranda *et al*. 2015). Indeed, the findings highlight that intensive agricultural landscapes are very relevant for guiña conservation and should not be dismissed as unsuitable.

Spatially, the occupancy dynamics of this carnivore appear to be affected by fragmentation and human pressure through land subdivision. Ensuring that remnant habitat patches are retained in the landscape, and land subdivision is reduced so that existing bigger farms are preserved, could ultimately safeguard the long-term survival of this threatened species. This should be the focus of conservation efforts, rather than just increasing the extent of habitat. Our findings further suggest that these remnant patches may play a key role in supporting the guiña in areas where there has been substantial habitat loss and, perhaps, might even offset local extinctions associated with habitat cover (Fahrig 2002). A land sharing scheme within agricultural areas of the landscape could prove to be a highly effective conservation strategy (Phalan *et al.* 2011) considering that these farms are currently not setting aside land, but are of high value to the species. The results also highlight that farmers with large properties are key stakeholders in the conservation of this species and must be at the centre of any conservation interventions that aim to protect existing native forest vegetation within farmland.

Following farming trends globally, larger properties in the agricultural areas of southern Chile are generally associated with high intensity production, whereas smaller farms are mainly subsistence-based systems (Carmona *et al.* 2010). It is therefore interesting, but perhaps counterintuitive, that we found occupancy to be higher (lower local extinction) where there is less land subdivision. However, a greater number of small farms is associated with higher human density which may result in increased persecution by humans (Woodroffe 2000). Also, higher subdivision imposes pressure on natural resources, due to more households being present in the landscape (e.g. Liu *et al.* 2003), which has been shown to reduce the quality of remaining habitat patches as a result of frequent timber extraction, livestock grazing (Carmona *et al.* 2010) and competition/interference by domestic animals and pets (Sepúlveda *et al.* 2014). Native vegetation in non-productive areas, including ravines or undrainable soils with a high water table, is normally spared within agricultural areas (Miranda *et al.* 2015), and these patches of remnant forest could provide adequate refuge, food resources and suitable conditions for carnivore reproduction (e.g. Schadt *et al.* 2002). However, it is possible that areas with high land subdivision and a large number of patches could be acting as ecological traps if source-sink dynamics are operating in the landscape (Robertson & Hutto 2006). Additionally, another factor driving the subdivision of land and degradation of remnant forest patches across agricultural areas is the growing demand for residential properties (Petitpas *et al.* 2017). This is facilitated by Chilean law, which permits agricultural land to be subdivided to a minimum plot size of 0.5 ha. Furthermore, it is common practice for sellers and buyers to completely eliminate all understory vegetation from such plots (C. Rios, personal communication) which, as demonstrated by detection being higher in dense understory, is a key component of habitat quality. The fact that farmers subdivide their land for economic profit, driven by demand for residential properties, is a very complex and difficult issue for future landscape-level conservation.

Although previous studies have suggested that human persecution may be a factor contributing to the decline of the guiña (Nowell & Jackson 1996; Sanderson, Sunquist & W. Iriarte 2002), illegal killing in the study region appears low and much less of a threat to the species than the habitat configuration in the landscape. Despite the fact that the species occupies a large proportion of the landscape across

442 seasons, people report that they rarely encounter the carnivore or suffer poultry predation. The guiña's
443 elusive behaviour is reinforced by our low camera-trap detection probability (p<0.2 over 2 nights).
444 One in ten respondents (10%) admitted to killing a guiña over the last decade. One potential drawback
445 of RRT is that it is impossible to know if people are following the instructions (Lensvelt-Mulders &
446 Boeije 2007). However, we deployed a symmetrical RRT design (both 'yes' and 'no' were assigned
447 as prescribed answers), which increases the extent to which people follow the instructions (Ostapczuk
448 & Musch 2011). Moreover, the proportion of 'yes' answers in the data exceeded the probability of
449 being forced to say 'yes' (which in this study was 0.167), indicating that respondents were reporting
450 illegal behaviour. From our data, it would be difficult to determine whether this prevalence of illegal
451 killing is having a detrimental impact on the population size of the species. However, with our
452 framework we could, in the future, evaluate spatial layers of information such as the probability of
453 illegal killing based on the distribution of encounters with the guiña and landscape attributes that
454 increase extinction probability (e.g. land subdivision and reduced habitat patches) in order to be
455 spatially explicit about where to focus conservation and research efforts (e.g. Santangeli *et al.* 2016).
456
457 Our results demonstrate the benefits of integrating socio-ecological data into a single modelling
458 framework to gain a more systematic understanding of the drivers of carnivore decline. The
459 framework teased apart the relative importance of different threats, providing a valuable evidence-
460 base for making informed conservation recommendations and prioritising where future interventions
461 should be targeted for the case study species. Prior to applying our framework, conservationists
462 believed that human persecution was instrumental in determining guiña occupancy patterns in human-
463 dominated landscapes. However, our combined socio-ecological approach highlighted that habitat
464 configuration/quality characteristics are the primary determinants, mainly due to the widespread
465 presence of the species across the landscape and lack of interaction with rural homes. The relative
466 importance of, and balance between, social and ecological factors may differ according to the species
467 of conservation concern. While our framework might not be to resolve conflict, it can help to guide
468 potential stakeholder controversies (Redpath *et al.* 2013; Redpath et al., 2017) by improving our
469 understanding of how carnivores interact with humans in space and time (Pooley *et al.* 2016). A

number of small to medium carnivores in need of research and conservation guidance (Brooke *et al.* 2014) could benefit from our framework.

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Figure Legends

Figure 1: Integrated socio-ecological modelling framework to assess drivers of carnivore decline in a human-dominated landscape.

Figure 2: Distribution of landcover classes and protected areas across the study landscape in southern Chile, including the forest habitat of our case study species, the guiña (*Leopardus guigna*). The two zones within which the 145 sample units (SU: 4 km^2) were located are indicated, with 73 SUs in the central valley (left polygon) and 72 within the Andes (right polygon). Illustrative examples of the variation in habitat configuration within SUs across the human-domination gradient are provided (bottom of image).

Figure 3: Predicted effects of forest cover, understory density, number of habitat patches and land subdivision on multi-season occupancy model parameters for the guiña (*Leopardus guigna*). These results correspond to the final selected model [ψ_1(Forest), *p*(season+Understory), ε(season+PatchNo+Subdivision), γ(season)]. Grey lines delimit 95% confidence intervals.

674 **Table 1:** Habitat configuration/quality and human relation predictors evaluated when modelling initial
675 occupancy (ψ_1), colonisation (γ), extinction (ε) and detection (p) probability parameters of multi-
676 season camera-trap guiña (*Leopardus guigna*) surveys. Further details can be found in Appendix S1,
677 S2 & Table S1.
678

Parameter	Predictor	Abbreviation in models
	Habitat configuration	
ψ_1, ε, γ	Percent of forest cover/habitat[†]	Forest
ψ_1, ε, γ	Percent shrub cover/marginal habitat	Shrub
ψ_1, ε, γ	Number of forest patches	PatchNo
ψ_1, ε, γ	Shape index forest patches	PatchShape
ψ_1, ε, γ	Forest patch size area[‡]	PatchAreaW
ψ_1, ε, γ	Forest patch continuity[‡]	Gyration
ψ_1, ε, γ	Edge length of forest land cover class	Edge
ψ_1, ε, γ	Landscape shape index of forest[§]	LSI
ψ_1, ε, γ	Patch cohesion[‡]	COH
	Human predator relations	
ψ_1, ε	Land subdivision	Subdivision
ψ_1, ε	Intent to kill (hypothetical scenario questions)	Intent
ψ_1, ε	Predation	Predation
ψ_1, ε	Frequency of predation	FQPredation
ψ_1, ε, p	Frequency of encounter[††]	FQEncounter
ψ_1, ε	Number of dogs	Dogs
	Habitat quality	
p	Bamboo density (*Chusquea* spp.)	Bamboo
p	Density of understory	Understory
p	Sample Unit rotation block	Rotation
p	Intensity of livestock activity	Livestock
p	Intensity of logging activity	Logging
p	Water availability	Water

679 [†]Pools together all forest types: old-growth, secondary growth, and wetland forest
680 [‡] Predictor excluded due to collinearity with percent of forest cover (Pearson's $|r|>0.7$)
681 [§] Predictor excluded due to collinearity with number of forest patches (Pearson's $|r|>0.7$)
682 [††] Predictor also fitted with detection probability
683
684
685

686 **Table 2:** The relationship between illegal killing of guiña (*Leopardus guigna*) and potential predictors
687 of the behaviour. Reported coefficients, standard errors, odds ratios and their 95% confidence
688 intervals were derived from a multivariate logistic regression which incorporates the known
689 probabilities of the forced RRT responses. Significance was accepted at the 0.05 level.
690

					Odds ratio	
	Coefficient	**SE**	**P**	**Odds ratio**	**Lower CI**	**Upper CI**
(Intercept)	-2.43	1.99	0.25	0.09	0.00	4.36
Age	-0.41	0.43	0.38	0.66	0.29	1.54
Income	0.00	0.55	0.99	0.99	0.34	2.96
Land parcel dependency	0.02	0.83	0.98	12.02	0.20	5.19
Number of chicken holdings	-0.18	0.71	0.78	0.83	0.21	3.38
Knowledge of legal protection	0.48	0.77	0.57	1.62	0.36	7.37
Frequency of encounter	0.85	0.50	0.04	2.34	0.87	6.28

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693 **Table 3:** Seasonal occupancy dynamics models following MacKenzie et. al. (2006), applied to the
694 guiña (*Leopardus guigna*), to define the base model structure for the subsequent model selection
695 procedure to evaluate potential habitat configuration/quality and human-predator predictors. Fitted
696 probability parameters are occupancy (ψ), colonisation (γ), extinction (ε) and detection (*p*). Models
697 assess whether changes in occupancy do not occur (model 1.6), occur at random (models 1.5, 1.4) or
698 follow a Markov Chain process (i.e. site occupancy status in a season is dependent on the previous
699 season) (models 1.0, 1.1, 1.2, 1.3). Initial occupancy (ψ_1) refers to occupancy in the first of four
700 seasons over which the guiña was surveyed. Model selection procedure is based on Akaike's
701 Information Criterion (AIC). ΔAIC is the difference in AIC benchmarked against the best model, w_i is
702 the model weight, K the number of parameters, and -2*loglike is the value of the log likelihood at its
703 maximum. The selected model is highlighted in bold.
704

Model	Seasonal dynamic models	ΔAIC	w_i	K	-2*loglike
1.0	ψ(.), γ(.), {ε= γ (1- ψ)/ψ}, *p*(season)	0.00	0.443	6	3982.93
1.1	**ψ_1(.), ε(season), γ(season), *p*(season)**	**0.36**	**0.370**	**11**	**3973.29**
1.2	ψ_1(.), ε(.), γ(.), *p*(season)	1.88	0.173	7	3982.81
1.3	ψ_1(.), ε(.), γ(.), *p*(.)	6.83	0.015	4	3993.76
1.4	ψ_1(.), γ(.),{ε= 1- γ}, *p*(season)	41.78	0.000	6	4024.71
1.5	ψ_1(.), γ(season),{ε= 1- γ}, *p*(season)	42.78	0.000	8	4021.71
1.6	ψ(.), {γ= ε= 0}, *p*(season)	104.11	0.000	6	4087.04

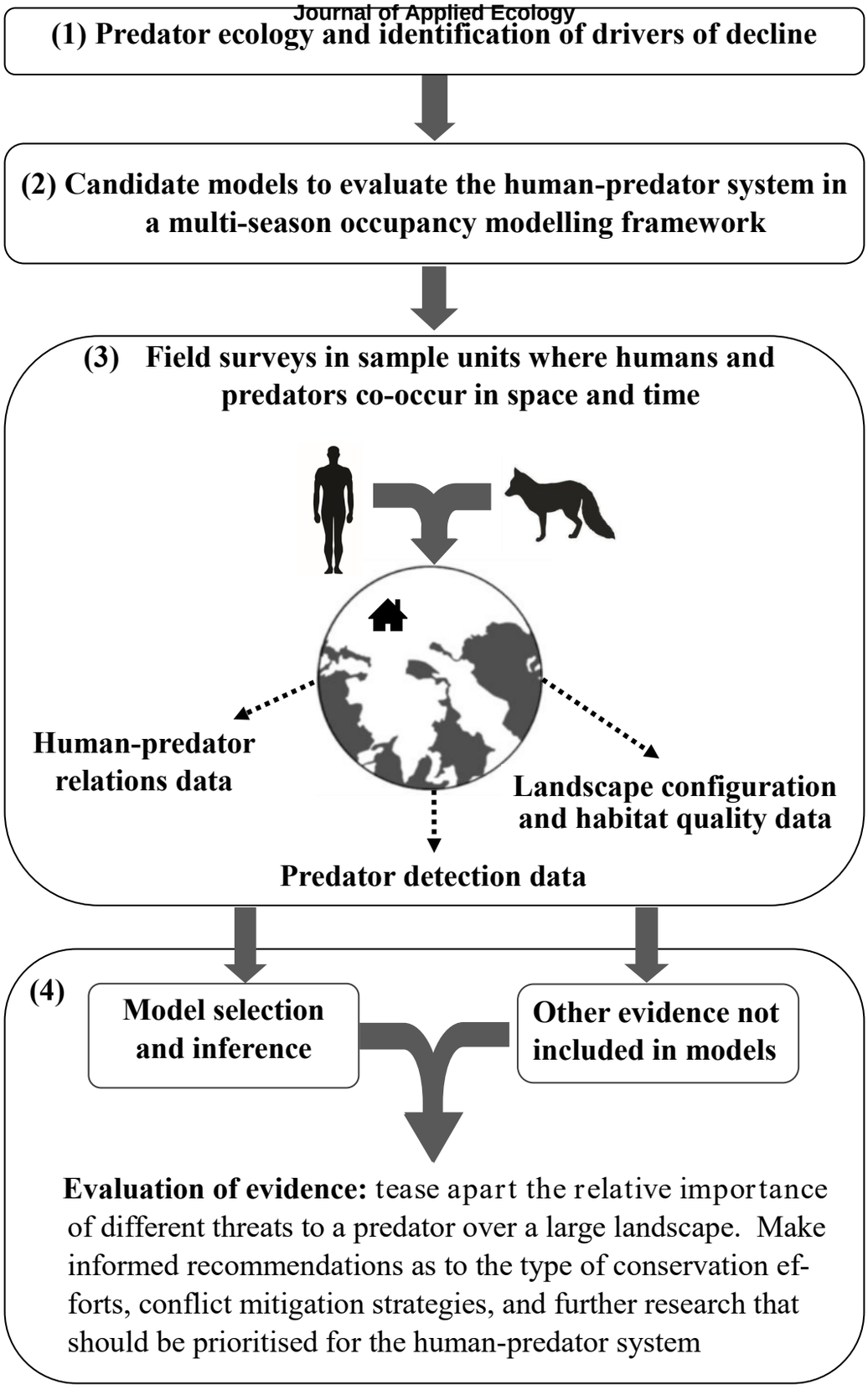
705
706

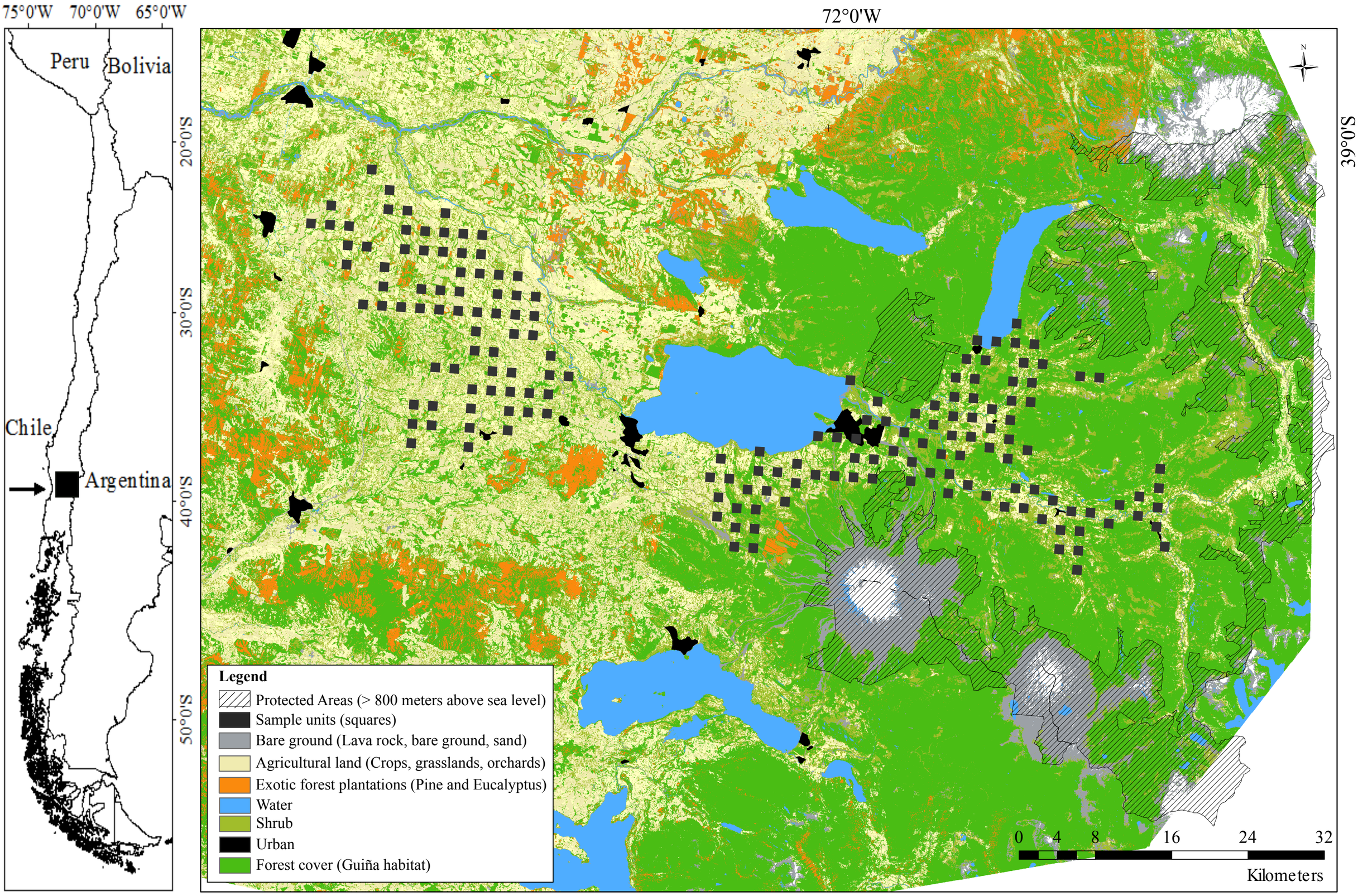
Table 4: Multi-season models of initial occupancy (ψ_1), extinction (ε), colonisation (γ) and detection (p) probability with potential habitat configuration/quality and human-predator predictors for the guiña (*Leopardus guigna*). Predictors were evaluated with a base model of seasonal dynamics [ψ_1(.), ε(season), γ(season), p(season)] using a step-forward model selection procedure and Akaike's Information Criterion (AIC). Initial occupancy (ψ_1) refers to occupancy in the first of four seasons over which the guiña was surveyed, with occupancy dynamics following a Markov Chain process. ΔAIC is the difference in AIC benchmarked against the best model, w_i is the model weight, K the number of parameters, and -2*loglike is the value of the log likelihood at its maximum. The selected models for each parameter are highlighted in bold and used in the next step. ε was fitted first followed by γ, then vice versa.

Model	Fitted parameter	ΔAIC	w_i	K	-2*loglike
	Detection/fitted with ψ_1(.), ε(season), γ(season)				
2.0	***p*(season+Understory)**	**0.00**	**0.9999**	**12**	**3934.47**
2.1	*p*(season+Bamboo)	18.48	0.0001	12	3952.95
	Initial occupancy/fitted with ε(season), γ(season), p(season+Understory)				
3.0	**ψ_1(Forest)**	**0.00**	**0.5425**	**13**	**3927.46**
3.1	ψ_1(Forest+Shrub)	1.24	0.2918	14	3926.7
3.4	ψ_1(PatchNo)	4.00	0.0734	13	3931.46
3.5	ψ_1(.)	5.01	0.0443	12	3934.47
3.6	ψ_1(Subdivision)	5.69	0.0315	13	3933.15
3.7	ψ_1(Dogs)	7.00	0.0164	13	3934.46
	Extinction first/fitted with ψ_1(Forest), p(season+Understory)				
4.0	**ε(season+PatchNo), γ(season)**	**0.00**	**0.4692**	**14**	**3920.10**
4.1	**ε(season+Subdivision), γ(season)**	**0.36**	**0.3919**	**14**	**3920.46**
4.2	ε(season+PatchShape), γ(season)	5.15	0.0357	14	3925.25
4.3	ε(season+Predation), γ(season)	5.24	0.0342	14	3925.34
4.4	ε(season), γ(season)	5.36	0.0322	13	3927.46
4.5	ε(season+FQencounter), γ(season)	5.92	0.0243	14	3926.02
4.6	ε(season+FQPredation), γ(season)	7.24	0.0126	14	3927.34

	Colonisation second/fitted with ψ_1(Forest), p(season+Understory) and 4.0/4.1 for ε				
4.7	**ε(season+PatchNo), γ(season)**	**0.00**	**0.1877**	**14**	**3920.10**
4.8	**ε(season+Subdivision), γ(season)**	**0.36**	**0.1568**	**14**	**3920.46**
4.9	ε(season+Subdivision), γ(season+PatchShape)	0.79	0.1265	15	3918.89
4.10	ε(season+PatchNo), γ(season+PatchShape)	1.29	0.0985	15	3919.39
4.11	ε(season+Subdivision), γ(season+PatchNo)	1.63	0.0831	15	3919.73
4.12	ε(season+PatchNo), γ(season+Edge)	1.84	0.0748	15	3919.94
4.13	ε(season+PatchNo), γ(season+Forest)	1.98	0.0698	15	3920.08
4.14	ε(season+Subdivision), γ(season+Edge)	2.16	0.0638	15	3920.26
4.15	ε(season+ Subdivision), γ(season+Forest)	2.20	0.0625	15	3920.30
4.16	ε(season+Subdivision), γ(season+Forest+Shrub)	3.50	0.0326	16	3919.60
4.17	ε(season+PatchNo), γ(season+Forest+Shrub)	3.60	0.0310	16	3919.70
4.18	ε(season), γ(season)	5.36	0.0129	13	3927.46
	Colonisation first/fitted with ψ_1(Forest), p(season+Understory)				
5.0	**ε(season), γ(season)**	**0.00**	**0.3303**	**13**	**3927.46**
5.1	ε(season), γ(season+PatchShape)	0.96	0.2044	14	3926.42
5.2	ε(season), γ(season+PatchNo)	1.55	0.1522	14	3927.01
5.3	ε(season), γ(season+Edge)	1.89	0.1284	14	3927.35
5.4	ε(season), γ(season+Forest)	1.95	0.1246	14	3927.41
5.5	ε(season), γ(season+Forest+Shrub)	3.41	0.06	15	3926.87
	Extinction second/fitted with ψ_1(Forest), p(season+Understory) γ(season)				
5.6	**ε(season+PatchNo+Subdivision), γ(season)**	**0.00**	**0.8275**	**15**	**3913.45**
5.7	ε(season+PatchNo), γ(season)	4.65	0.0809	14	3920.10
5.8	ε(season+Subdivision), γ(season)	5.01	0.0676	14	3920.46
5.9	ε(season+PatchShape), γ(season)	9.80	0.0062	14	3925.25
5.10	ε(season+Predation), γ(season)	9.89	0.0059	14	3925.34
5.11	ε(season), γ(season)	10.01	0.0055	13	3927.46
5.12	ε(season+FQEncounters), γ(season)	10.57	0.0042	14	3926.02
5.13	ε(season+FQPredation), γ(season)	11.89	0.0022	14	3927.34

717

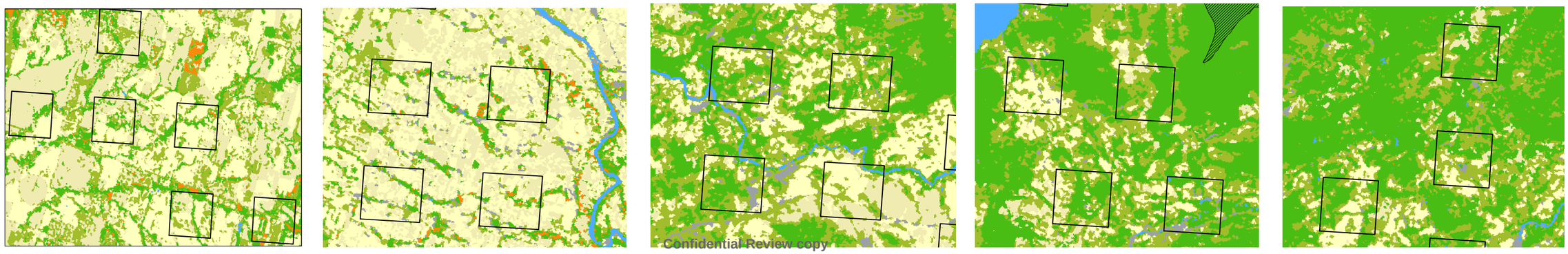

(1) Predator ecology and identification of drivers of decline
(2) Candidate models to evaluate the human-predator system in a multi-season occupancy modelling framework
(3) Field surveys in sample units where humans and predators co-occur in space and time
Human-predator relations data
Landscape configuration and habitat quality data
Predator detection data
(4)
Model selection and inference
Other evidence not included in models
Evaluation of evidence: tease apart the relative importance of different threats to a predator over a large landscape. Make informed recommendations as to the type of conservation efforts, conflict mitigation strategies, and further research that should be prioritised for the human-predator system

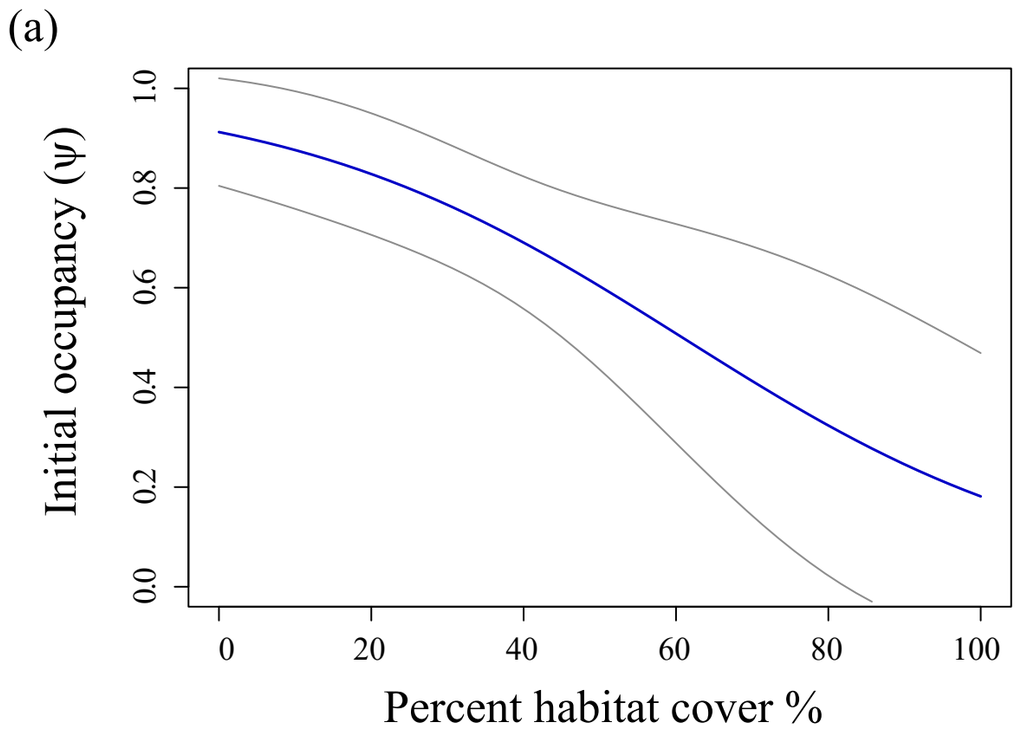


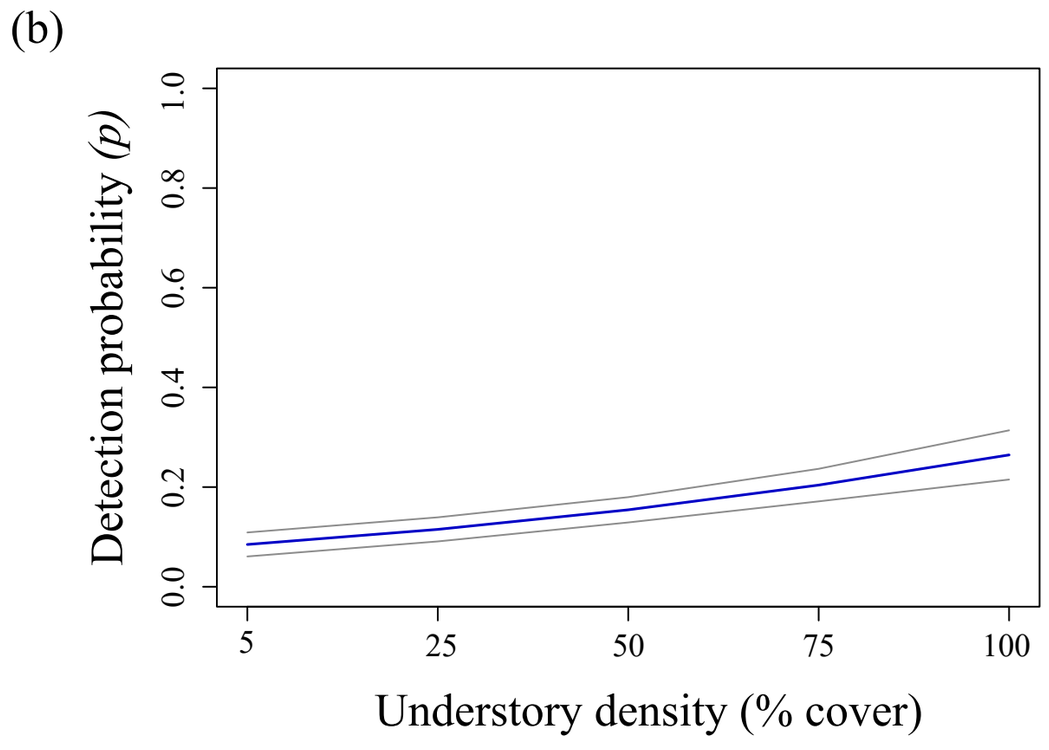
Central Valley

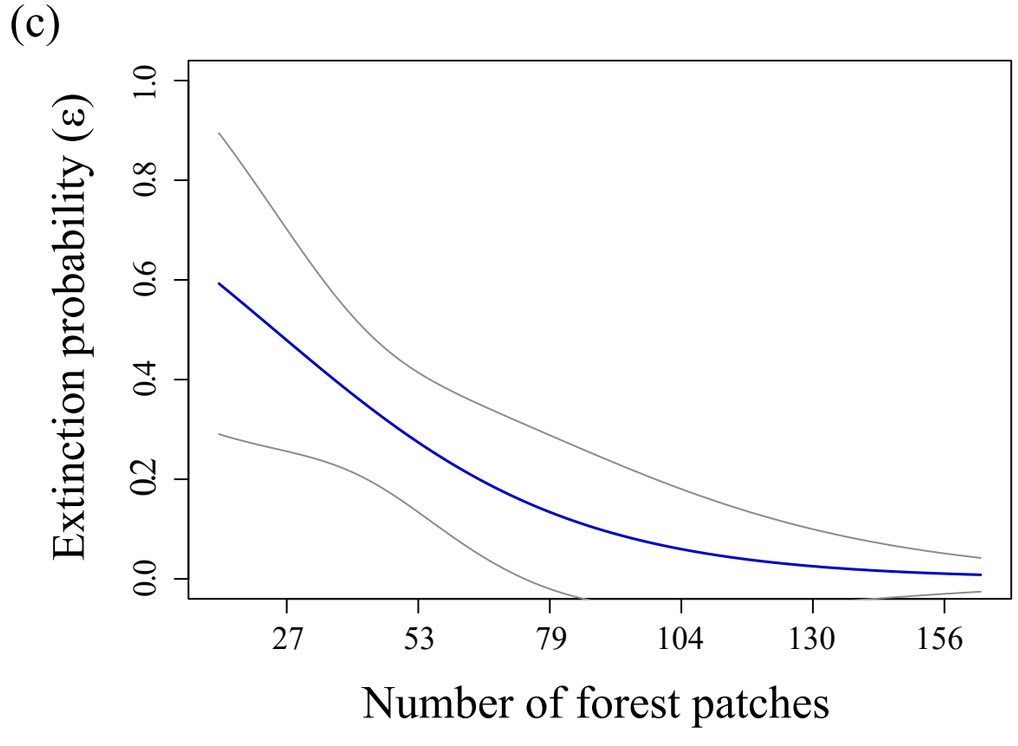
Andean Valleys

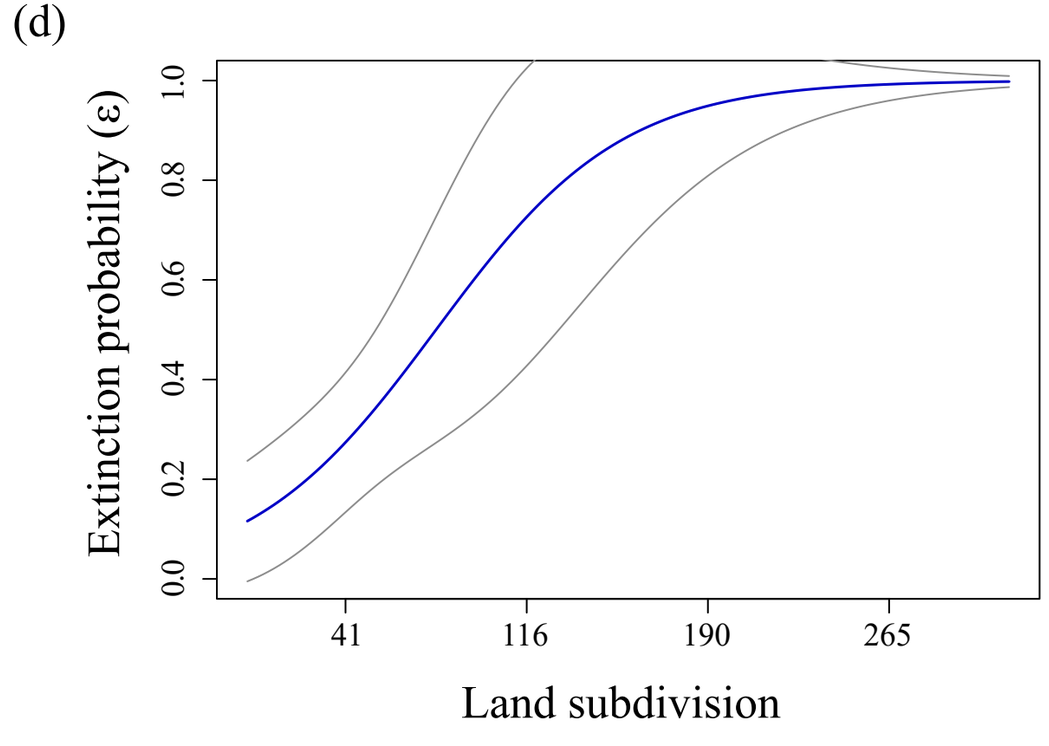
Examples of sample units accross the gradient




(a)
Initial occupancy (ψ)
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100
Percent habitat cover %


(b)
Detection probability (p)
0.0
0.2
0.4
0.6
0.8
1.0
5
25
50
75
100
Understory density (% cover)


(c)
Extinction probability (ε)
0.0
0.2
0.4
0.6
0.8
1.0
27
53
79
104
130
156
Number of forest patches


(d)
Extinction probability (ε)
0.0
0.2
0.4
0.6
0.8
1.0
41
116
190
265
Land subdivision

Supporting Information

Appendix S1: Landcover classification of study area

Landcover classification was carried out using a composite of four Aster images at 15 m resolution from between 2002 and 2007. Native forest cover within the study region did not change significantly between 1983 and 2007 (Petitpas 2017; Miranda *et al.* 2015). In addition, the current extent and configuration of forest across the sample units (SUs) has not altered perceptibly when compared visually with up-to-date Google Earth imagery from 2014. The study region was categorised into nine landcover classes ((i) water; (ii) forest, (iii) forest regrowth, (iv) shrub/bog, (v) grassland, (vi) hualve (inundated forests), (vii) plantation, (viii) crop/pasture/orchard and (ix) bare ground/sand/lava rock) using a supervised classification with maximum likelihood estimation, based on field data from 738 training points. A further 738 points were used to verify classification accuracy, which was 'almost perfect' (Kappa= 0.81 (SE= 0.017); Landis & Koch 1977; Congalton 1991). Urban landcover digitised by hand and added as a tenth class. Image processing and classification were conducted in ERDAS Imagine 2014 (Hexagon Geospatial, Norcross, GA, USA) and ArcMap v.10.1 (ESRI, Redlands, CA, USA).

Appendix S2: Generation of the human-predator relations data, used as potential predictors to model multi-season occupancy dynamics of the guiña (*Leopardus guigna*)

The questionnaire delivery and design were approved by School of Anthropology and Conservation Research and Research Ethics Committee, University of Kent, as well as the Villarrica Campus Committee of the Pontificia Universidad Católica de Chile. All householders were fully informed of the study objectives, but with care taken to ensure that the information provided would not lead to (un)conscious bias in the participant's responses. The contact and employment details for the principal researcher were provided in case any unforeseen issues were experienced after completing the questionnaire. The respondents were told that their engagement in the research was entirely voluntary and that they could withdraw from the process at any point, without needing to provide an explanation. Additionally, they were notified that their answers to the questionnaire would be anonymised and only ever presented in aggregate form, so their identity would not be discernible. The respondents were also assured that the data would be stored securely, only accessible by the lead researcher and would not be passed on to any second parties, in line with the UK Data Protection Act. Each individual was then given time to evaluate all this information, prior to signing an informed consent sheet.

The questionnaire consisted of six sections. The first part included socio-demographic/economic questions relating to age, amount of schooling, livelihood activities and income. The next section focussed on questions regarding killing wild animals, including species with protected (e.g. puma, guiña) and non-protected status (e.g. introduced wild boar). To prevent any bias in responses, our questions included all native carnivores known to occur across the study region, as well as free-roaming domestic dogs. As killing of protected species is an illegal activity, we employed the Randomised Response Technique (RRT) described in St John et al. (2010). A dice was used as randomisation tool; respondents were asked to provide a truthful answer if they rolled a one, two, three or four, must answer "yes" if they rolled a five (irrespective if it is true answer or not) and must answer "no" if the dice landed on six. The time period used to provide context to the question was 'over the last ten years', which was deemed most appropriate after the pilot exercise. Trial runs were

conducted using non-sensitive questions to ensure the RRT instructions were understood and being followed by the respondents. A visual barrier was used to ensure that the interviewer could not see the number on the rolled dice.

The third part of the questionnaire asked respondents to report livestock losses via predation over the past year, or an alternative time period they could quantify. In the fourth section, participants were probed about their knowledge of whether the hunting of each species was permitted or illegal, as well as asking how frequently the species were encountered. A fifth section aimed to evaluate scenarios of predation with a hypothetical livestock holding of 100 sheep and chickens. Respondents were asked what behaviour they would display towards the carnivores occurring in the study region after a specific level of predation (2, 10, 25, 50, >50 sheep or chickens) has been experience. For sheep predation, we assessed the puma (*Puma concolor*) and domestic dogs (*Canis familiaris*), and for chicken predation we asked about guiña and Harris hawk (*Parabuteo unicinctus*). In order not to bias responses, respondents were offered a choice of possible actions (e.g. lethal controls, call authorities, improve management, nothing, etc.). The value of this hypothetical predation scenario was interpreted as a measure to tolerance to predation. The final section centred on the management of livestock, particularly sheep and chickens, in relation to behaviour such as enclosing livestock at night, the distance of the closure from household, the number of domestic dogs/cats associated with the property and how they are managed overnight (e.g. free-roaming, tethered), as well as how often they are fed and the type of food they are given.

68 The original (Spanish) and translated (English) questions were as follows:

RANDOMISED RESPONSE (RRT)	**Response Type**
1. During the last 10 years, have you killed a wildboar? En los últimos diez años ha matado a un Jabalí?	Yes/No
2. During the last 10 years, have you killed a puma? En los últimos diez años ha matado a un puma?	Yes/No
3. During the last 10 years, have hired someone to kill a puma? En los últimos diez años ha matado a contratado a alguien para matar a un puma?	Yes/No
4. During the last 10 years, have you killed a guiña? En los últimos diez años ha matado a una guiña?	Yes/No
5. During the last 10 years, have you killed a fox? En los últimos diez años ha matado a un zorro?	Yes/No
6. During the last 10 years, have you killed a hawk? En los últimos diez años ha matado a un peuco?	Yes/No
7. During the last 10 years, have you killed a rabbit or hare? En los últimos diez años ha matado a un conejo o liebre?	Yes/No
8. During the last 10 years, have you killed a free roaming domestic dog not of your ownership? En los últimos diez años ha matado a un perro doméstico andariego que no es de su propiedad?	Yes/No
9. During the last 10 years, have you killed a weasel? En los últimos diez años ha matado a un quique?	Yes/No
10. During the last 10 years, have you killed a skunk? En los últimos diez años ha matado a un chingue?	Yes/No
HOUSEHOLD INFORMATION	
11. What is the size of your property in hectares? Cuál es el tamaño de su propiedad?	*Exact figure*

12. How long have you lived here? Where are you originally from? Hace cuánto vive en el sector? De donde es?	*Exact figure*
13. What is your age? And that of other adults in the household? Cuál es la edad de los adultos del hogar? (dueños de casa)	*Exact figure*
14. What is your level of schooling? And that of other adults in the household? Cuál es el nivel escolar de los adultos del hogar? (dueños de casa)	*Exact figure*
15. How many children do you have? Cuantos hijos tiene?	*Exact figure*
16. Please classify in order of importance the following economic activities for your overall income? Clasifique en orden de importancia para su ingreso familiar las siguientes actividades económicas?	Crops/Livestock/Forestry/Urban services/ Agricultural services/Tourism/Subdivision of land for residential development/Other
17. What is your approximate monthly income? Cuál es su ingreso mensual aproximado?	*Exact figure*
PREDATION OF DOMESTIC ANIMALS	
18. What are your livestock animal holdings during the past year? Cuantos animales ha tenido durante el año pasado?	Bovine/Ovine/Chickens/Others
19. How many livestock animals have you lost because of this predator in the past year? If respondent could not quantify over the past year their alternative time period was noted (e.g. 3 sheep killed by puma in 5 years) Cuántos animales ha perdido por parte del predador? Si el entrevistado no podía cuantificar en un año, entonces se anotaba el periodo de tiempo en el cual sufrió un numero de pérdida (e.g. 3 ovejas predadas por puma en 5 años) *The question was repeated in turn for the following predators: puma, guiña, fox, hawk, domestic dogs, skunk, weasel* *La pregunta fue repetida para puma, guiña, zorros, peucos (rapaces diurnas), perros domésticos, chingues y quique.*	*Exact figure*
KNOWLEDGE OF PREDATOR LEGAL STATUS	
20. From your knowledge, is hunting this predator prohibited? Según su conocimiento, se puede cazar al animal? *The question was repeated in turn for the following predators:* puma, guiña, fox, hawk, domestic dogs, skunk, weasel, hare-rabbit La pregunta fue repedita para puma, guiña, zorros, peucos (rapaces diurnas), perros domésticos, chingues, quique y liebre y conejos	Yes/No/Do not know

FREQUENCY OF PREDATOR ENCOUNTERS	
21. How frequently do you observe a sign or sound indicating that this predator has been on your property? Please use a unit of time that you can remember (daily, weekly, monthly, yearly) Con que frecuencia observa (o algún indicio) al animal en su propiedad? Use una medida de tiempo que recuerde (diario, semanal, mensual, anual). *The question was repeated in turn for the following predators:* puma, guiña, fox, hawk, domestic dogs, skunk, weasel, hare-rabbit La pregunta fue repedita para puma, guiña, zorros, peucos (rapaces diurnas), perros domésticos, chingues, quique y liebre y conejos	*Exact figure*
SCENARIO-BASED QUESTION: HYPOTHETICAL RESPONSE TO PREDATION	Open ended question with internal codes for: (1)Call authorities; (2)Intent to hunt it; (3)Capture and call authorities; (4)Scare off; (5)Nothing; (6)Observe; (7)Protect my livestock holdings; (8)other
"Let's suppose that you have 100 sheep" / "Digamos que usted tiene 100 ovejas"	
22. What do you think you would do if the puma kills X/100 Sheep Qué haría si un puma le mata X/100 ovejas? X = 2, 10, 25, 50, >50	Internal code
23. What do you think you would do if a domestic dog kills X/100 sheep Qué haría si un perro doméstico le mata X/100 ovejas? X = 2, 10, 25, 50, >50	Internal code
"Let's suppose that you have 100 Sheep" / "Digamos que usted tiene 100 Ovejas"	
24. What do you think you would do if the guiña kills X/100 chickens? Qué haría si un guiña le mata X/100 chickens? X = 2, 10, 25, 50, >50	Internal code
What do you think you would do if a hawk kills X/100 chickens? Qué haría si un peuco (todas las rapaces diurnas) le mata X/100 gallinas? X = 2, 10, 25, 50, >50	Internal code

DOMESTIC ANIMAL MANAGEMENT	
25. How do you keep your livestock animals at night? Como guarda sus animales durante la noche? Question asked for sheep and chickens Pregunta realizada para ovejas y gallinas	Closed housing/Open corral/Open field with dog/Open field without dog/Other, how?
26. At what distance do you keep your livestock animals at night? meters A que distancia de su casa guarda sus animales durante la noche? metros Question asked for sheep and chickens Pregunta realizada para ovejas y gallinas	*Exact figure*
27. How many dogs/cats do you have? Cuantos perros/gatos tienen en su casa?	*Exact figure*
28. What do you do with your dogs/cats at night? Que hace con sus perros/gatos durante la noche?	Enclosure/Tied/Free-roaming/Other
29. With what do you feed your dog/cat? Con que alimenta a sus perros/gatos?	Commercial pellets/Kitchen scraps/Mix of pellets and kitchen scraps/Grain/Mix of grain and kitchen scraps/Nothing/Other

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Table S1: Description of potential habitat configuration/quality and human-predator predictors used when modelling initial occupancy (ψ_1), colonisation (γ), extinction (ε) and detection (p) probability parameters from multi-season camera-trap surveys of the guiña (*Leopardus guigna*). Detailed description of habitat configuration metrics can be found in (McGarigal *et al.* 2002).

Predictor	**Abbreviation in models**	**Description**[§§]
Habitat configuration		
Percent forest cover	Forest	Metric that measures habitat loss as the extent of forest cover in a sample unit (0-100). Forest cover was obtained by pooling old-growth and secondary forest landcover classes, which are both considered to be suitable guiña habitat (Nowell & Jackson 1996; Acosta-Jamett & Simonetti 2004).
Percent shrub cover	Shrub	Metric that measures the extent of shrub cover in a sample unit (0-100). The spatial configuration is not assessed because shrub is a marginal habitat and evaluated for an additive effect on forest cover. As shrub can be considered a marginal habitat for guiña (Dunstone *et al.* 2002; Sanderson, Sunquist & W. Iriarte 2002; Acosta-Jamett & Simonetti 2004), we also measured the extent of shrub cover to evaluate possible additive effects with habitat cover
Number of forest patches	PatchNo	Metric that measures the number of forest habitat patches (0-∞).
Shape index forest patches	PatchShape	Shape metric that measures the complexity of forest habitat patch shape compared to a square, weighted for the entire landscape. As the index value increases, that habitat patch shape is more irregular (1-∞).
Forest patch size area[†]	PatchAreaW	Metric that measures mean habitat patch area (0-∞) corrected for sample unit scale. It provides a landscape centric perspective of patch structure.
Forest patch continuity[†]	Gyration	Metric that measures habitat patch continuity (0-∞). It can be interpreted as the average distance an organism can move within the habitat before an edge is encountered (McGarigal *et al.* 2002). The value increases with greater habitat patch extent.

Edge length of forest	Edge	Area-edge metric that measures the total length (0-∞) of habitat patch edge across a sample unit. This can be used instead of edge density because we are comparing sample units of the same size (McGarigal *et al.* 2002). The value rises with increasing edge.
Landscape shape index of forest[‡]	LSI	Aggregation metric that compares the landscape level edge of the habitat to one without internal edges or a square (0-100). This is a measure of the level of fragmentation in a sample unit.
Patch Cohesion[†]	COH	Aggregation metric that measures the physical connectedness (0-1) of forest habitat cover by measuring the aggregation of patches.
Human-predator relations data		
Land subdivision	Subdivision	Measures the number of land tenure divisions (i.e. owners) in a sample unit (0-∞). We expect higher subdivision to represent greater anthropogenic pressure and management variability from factors such as logging and presence of domestic dogs which were not measured directly in each sample unit (e.g. Theobald, Miller & Hobbs 1997; Hansen *et al.* 2005; Western, Groom & Worden 2009). Subdivision was based on the number of properties or land parcels recorded in each SU from national records (CIREN-CORFO, 1999).
Intent to kill	Intent	Intent to kill guiña by households in a sample unit (categorical: yes= 1, no= 0). This measure describes how a respondent states they would respond if a guiña two of their chickens. It is a highly conservative indicative measure of tolerance to livestock predation before lethal control is considered.
Predation	Predation	Occurrence of chicken predation by guiña in a sample unit (categorical: yes= 1, no= 0).
Frequency of predation	FQPredation	Frequency of chicken predation by guiña in a sample unit. Predation events were scaled to yearly frequency (0-∞).
Frequency of encounter[§]	FQEncounter	Numbers of encounters householders have had with guiña, scaled to a yearly frequency (0-∞). Frequency of encounters is also used to fit detection probability as a proxy for the elusiveness of the species.

Number of dogs	Dogs	Maximum number of free-roaming dogs, owned by the household, at night in proximity to the camera-traps (0-∞). We assume this value to be a conservative proxy to dog activity and an index of interference/competition by dogs. We also fitted extinction probability with free roaming dogs as they have been documented to interfere and kill wildlife in Chile (Silva-Rodriguez, Ortega-Solis & Jimenez 2010; Silva-Rodríguez & Sieving 2012), therefore we included average number of free roaming domestic dogs of nearby households (from our questionnaire Appendix S2 as a potential source of mortality. Because guiña are mainly nocturnal (Delibes-Mateos *et al.* 2014; Hernandez *et al*. 2015) we excluded households that restrain dogs at night.
Habitat quality and survey specific variables[§]		
Bamboo density (*Chusquea* spp.)	Bamboo	Bamboo density (*Chusquea* spp.) within a 25 m radius of each camera-trap, recorded in five categorical percentage classes (Braun-Blanquet 1965).
Density of understory	Understory	Understory vegetation density within a 25 m radius of each camera-trap, recorded in five categorical percentage classes (Braun-Blanquet 1965).
SU rotation	Rotation	Each SU was included in one of four consecutively sampled rotations of camera-traps during each season.
Intensity of livestock activity	Livestock	Livestock activity next to each camera-trap visually assessed and recorded using three categories (high, medium or low intensity). Based on signs such as presence of animals, grazed vegetation, trampled paths and manure.
Intensity of logging activity	Logging	Logging activity next to each camera-trap visually assessed and recorded using three categories (high, medium or low intensity). Based on signs such as active firewood piles, clearings, logging paths, fresh stumps and fallen logs.
Water availability	Water	The availability of water was recorded as either present or absent at the patch level during each season (categorical: yes= 1, no= 0).

[†]Predictor excluded due to collinearity with percent of forest cover (Pearson's $|r|>0.7$)

[‡]Predictor excluded due to collinearity with number of forest patches (Pearson's $|r|>0.7$)

[§]Predictors fitted only with detection probability at the forest patch level

[§§] Supporting information references:

Braun-Blanquet, J. (1965) Plant Sociology: The Study of Plant Communities. Hafner, London.
CIREN (Centro de Información de Recursos Naturales), CORFO (Corporación de Fomento), 1999. Digital Cartography of Rural Properties.
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Multi-season occupancy modelling framework to assess socio-ecological drivers of carnivore decline

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Summary

1. Habitat loss, fragmentation and degradation resulting from land-use change are key threats to the long-term persistence of carnivores, which are also susceptible to direct persecution by people. Integrating natural and social science methods to examine how habitat configuration/quality and human-predator relations may interact in space and time to effect carnivore populations existing within human-dominated landscapes will help to prioritise conservation investment and action effectively.
2. We propose a socio-ecological multi-season occupancy modelling framework to evaluate drivers of carnivore decline in landscapes where predators and people coexist. Candidate models can be used to quantify and tease apart the relative importance of different threats.
3. We apply our methodological framework to an empirical case study, the threatened guiña (*Leopardus guigna*) in the temperate forest ecoregion of southern Chile, to illustrate its use. The existing literature suggests that the species is declining due to habitat loss, fragmentation and persecution in response to livestock predation. Data used in modelling were derived from four seasons of camera-trap surveys, remote-sensed images and household questionnaires.
4. Occupancy dynamics were explained by habitat configuration/quality covariates rather than by human-predator relations. Guiñas can tolerate a high degree of habitat loss. They are primarily impacted by fragmentation and land subdivision (larger farms being broken up into smaller ones). Ten percent of surveyed farmers (N=233) reported illegally killing the species over the past decade.
5. *Synthesis and applications*. By integrating ecological and social data into a single modelling framework, our study demonstrates the value of an interdisciplinary approach to assessing the potential threats to a carnivorous mammal. It has allowed us to tease apart effectively the relative importance of different potential extinction pressures, make informed conservation recommendations and prioritise where future interventions should be targeted. Specifically in relation to the guiña, we have identified that human-dominated landscapes with large intensive farms can be of conservation value, as long as an appropriate network of habitat patches are maintained within the matrix. Conservation efforts to secure the long-term

persistence of the species should focus on reducing habitat fragmentation, rather than human persecution in our study system.

Key-words: agriculture, camera-trapping, conservation, randomised response technique, habitat fragmentation, habitat loss, human-predator relations, human-wildlife co-existence, illegal killing, *Leopardus guigna*

Introduction

Land-use change is one of the greatest threats facing terrestrial biodiversity globally (Sala *et al.* 2000), as species persistence is negatively influenced by habitat loss, fragmentation, degradation and isolation (Henle *et al.* 2004a). In general, species characterised by a low reproductive rate, low population density, large individual area requirements or a narrow niche are more sensitive to habitat loss and fragmentation (Fahrig 2002; Henle *et al.* 2004b) and, therefore, have a higher risk of extinction (Purvis *et al.* 2000). As a consequence, many territorial carnivores are particularly vulnerable to land-use change. Furthermore, the disappearance of such apex predators from ecosystems can have substantial cascading impacts on other species (Estes *et al.* 2011; Ripple *et al.* 2014).

Additionally, in human-dominated landscapes, mammal populations are threatened directly by the behaviour of people (Ceballos *et al.* 2005). For instance, larger species (body mass >1 kg) are often persecuted because they are considered a pest, food source or marketable commodity (Woodroffe, Thirgood & Rabinowitz 2005). Carnivores are especially vulnerable to persecution after livestock predation, attacks on humans, or as a result of deep rooted social norms or cultural practices (Treves & Karanth 2003; Inskip & Zimmermann 2009; Marchini & Macdonald 2012). Indirectly, many mammals are also threated by factors such as the introduction of invasive plant species, which reduce habitat complexity (Rojas *et al.* 2011), and domestic pets, which can transmit diseases or compete for resources (Hughes & Macdonald 2013).

To ensure the long-term future of carnivore populations within human-dominated landscapes outside protected areas, it is imperative that we identify potential ecological and social drivers of species decline and assessing their relative importance (Redpath *et al.* 2013). For example, it is essential to disentangle the impacts of habitat loss and fragmentation on a species, as the interventions required to alleviate the pressures associated with the two processes are likely to be different (Fahrig 2003; Fischer & Lindenmayer 2007). If habitat loss is the dominant issue causing population reduction, then large patches may need to be protected to ensure long-term survival, whereas a certain configuration of remnant vegetation may be imperative if fragmentation is the main threat. At the same time, it is important to understand if, how and why people persecute species, if conservationists are to facilitate human-wildlife coexistence (St John, Keane & Milner-Gulland 2013). However, there is a paucity of interdisciplinary research that evaluates explicitly both ecological and social drivers of species decline in a single coherent framework, across geographic scales pertinent to informing conservation decision-making (Dickman 2010).

From an ecological perspective, data derived from camera-traps and analysed via occupancy models are widely used to study carnivores over large geographic areas (Burton *et al.* 2015; Steenweg *et al.* 2016). Occupancy modelling offers a flexible framework that can account for imperfect detection and missing observations, making it highly applicable to elusive mammals of conservation concern (MacKenzie *et al.* 2003; MacKenzie & Reardon 2013). Dynamic (i.e. multi-season) occupancy models are particularly useful because they examine trends through time and can be used to ascertain the factors underlying observed changes in occupancy (MacKenzie *et al.* 2003, 2006). Similarly, there are a range of specialised social science methods for asking sensitive questions that can be used to yield valuable information on human behaviour, including the illegal killing of species (Nuno & St. John 2015). These include the unmatched count technique, recently used to study hunting inside Serengeti National Park, Tanzania (Nuno *et al.* 2013) and bird hunting in Portugal (Fairbrass *et al.* 2016), as well as the randomised response technique (RRT), previously used to estimate the prevalence of predator persecution in South Africa (St John *et al.* 2012) and vulture poisoning in Namibia (Santangeli *et al.* 2016).

111

112 In this paper, we propose an integrated socio-ecological modelling framework that draws together
113 these natural and social science methods to examine how habitat configuration/quality and human-
114 predator relations may interact in space and time to effect carnivore populations across a human-
115 dominated landscape. We showcase the approach using the guiña (*Leopardus guigna*), an
116 International Union for Conservation of Nature (IUCN) Red Listed felid, as a case study species.
117 Specifically, we use data derived from multi-season camera-trap surveys, remote-sensed images and a
118 household questionnaire which uses RRT to estimate prevalence and predictors of illegal killing. The
119 outputs from the modelling framework provide a robust evidence-base to direct future conservation
120 investment and efforts.

121

122 **Methods**

123 ***Integrated socio-ecological framework***

124 Our proposed a modelling framework comprises four stages (Fig. 1). The first step is to gather
125 information on the ecology of the species and likely drivers of decline, including habitat
126 configuration/quality issues (e.g. habitat loss, habitat fragmentation, presence/absence of habitat
127 requirements) and human-predator relations (e.g. species encounter frequency, livestock predation
128 experiences), that require evaluation. The best available information can be acquired from sources
129 such as peer-reviewed and grey literature, experts and IUCN Red List assessments. The next task, step
130 two, is to define a suite of candidate models *a priori* to assess and quantify the potential social and
131 ecological predictors on species occupancy dynamics. Dynamic occupancy models estimate
132 parameters of change across a landscape, including the probability of a sample unit (SU) becoming
133 occupied (local colonisation) or unoccupied (local extinction) over time (MacKenzie *et al.* 2006).

134

135 The third step involves the collection of ecological and social data in SUs distributed across the
136 landscape, to parametise the models. Camera-trap survey effort allocation (i.e. the number of SUs that
137 need to be surveyed) for occupancy estimation can be determined *a priori* using freely-available tools
138 (Gálvez *et al.* 2016). The final stage is the evaluation of evidence, using standard model selection

methods (Burnham & Anderson 2002) to establish which of the social and ecological variables within the candidate models are indeed important predictors of occupancy, and to contrast their relative importance. Results from the models can be contextualised with additional supporting evidence not embedded in the models to inform where conservation action should be directed. For instance, during questionnaire delivery, valuable qualitative data may be recorded that provides in-depth insights related to the human-predator system (e.g. Inskip *et al.* 2014).

Study species and system

The guiña is the smallest neotropical felid (<2 kg) and is categorised as Vulnerable by the IUCN (Napolitano *et al.* 2015). It is thought to require forest habitat with dense understory and the presence of bamboo (*Chusquea* spp.) (Nowell & Jackson 1996; Dunstone *et al.* 2002), but is also known to occupy remnant forest patches within agricultural areas (Sanderson, Sunquist & W. Iriarte 2002; Acosta-Jamett & Simonetti 2004; Gálvez *et al.* 2013; Fleschutz *et al.* 2016; Schüttler *et al.* 2017). Guiñas are considered pests by some people as they can predate chickens and, while the extent of persecution has not been formally assessed, killings have been reported (Sanderson, Sunquist & W. Iriarte 2002; Gálvez *et al.* 2013). Killing predominately occurs when the felid enters a chicken coop (Gálvez & Bonacic 2008). Due to these attributes, the species makes an ideal case study to explore how habitat configuration/quality and human-predator relations may interact in space and time to influence the population dynamics of a threatened carnivore existing in a human-dominated landscape.

The study was conducted in the Araucanía region in southern Chile (Fig. 2), at the northern limit of the South American temperate forest eco-region (39º15´S, 71º48´W) (Armesto *et al.* 1998). The system comprises two distinct geographical sections common throughout Southern Chile: the Andes mountain range and central valley. Land-use in the latter is primarily intensive agriculture (e.g. cereals, livestock, fruit trees) and urban settlements, whereas farmland in the Andes (occurring <600 m.a.s.l) is less intensively used and surrounded by tracks of continuous forest on steep slopes and protected areas (>800 m.a.s.l). The natural vegetation across the study landscape consists of deciduous

and evergreen *Nothofagus* forest (Luebert & Pliscoff 2006), which remains as a patchy mosaic in agricultural valleys and as continuous tracts at higher elevations within the mountains (Miranda *et al.* 2015).

Data collection

Predator detection/non-detection data

We obtained predator detection/non-detection data via a camera-trap survey. Potential SUs were defined by laying a grid of 4 km^2 across the study region, representing a gradient of forest habitat fragmentation due to agricultural use and human settlement below 600 m.a.s.l. The size of the SUs was informed by mean observed guiña home range size estimates of collared individuals in the study area (MCP 95% mean=270 ±137 ha; Schüttler *et al.* 2017).

In this study system, detectability was modelled based on the assumption that a two-day survey block is a separate independent sampling occasion. This time threshold was chosen because individuals do not stay longer than this time in any single location (Schüttler et al. unpublished data). Minimum survey effort requirements (i.e. number of SUs and sampling occasions) were determined following Guillera-Arroita, Ridout & Morgan (2010), using species specific parameter values from Gálvez *et al.* (2013) and a target statistical precision in occupancy estimation of SE<0.075. A total of 145 SUs were selected at random from the grid of 230 cells, with 73 and 72 located in the central valley and Andes mountain valley respectively (Fig. 2). The Andean valleys were surveyed for four seasons (summer 2012, summer 2013, spring 2013, summer 2014), while the central valley was surveyed for the latter three seasons. A total of four rotations (i.e. blocks of camera-traps) were used to survey all SUs within a 100-day period each season. Detection/non-detection data were thus collected for 20-24 days per SU, resulting in 10-12 sampling occasions per SU. Two camera-traps (Bushnell ™trophy cam 2012) were used per SU, positioned 100-700 m apart, with a minimum distance of >2 km between camera-traps in adjacent SUs. The detection histories of both camera-traps in a SU were pooled, and camera-trap malfunctions or thefts (five in total) were treated as missing observations.

195 *Habitat configuration/quality data*

196 The extent of habitat loss and fragmentation were evaluated using ecologically meaningful metrics
197 which have been reported in the literature as being relevant to guiñas, using either field or remote-
198 sensed landcover data (Table 1 and Supplementary Information Appendix S1 & Table S1). The
199 metrics were measured within a 300 ha circular buffer, centred on the midpoint between both cameras
200 in each SU using FRAGSTATS 4.1 (McGarigal *et al.* 2002). Habitat quality surrounding a camera-
201 trap might influence species activity (Acosta-Jamett, Simonetti, 2004). We collected data on a number
202 of variables within a 25-m radius around each camera-trap (Table S1), as this is deemed to be the area
203 over which localised conditions may influence species detectability. The habitat quality data from
204 both camera-traps in each SU were pooled and the median was used if values differed.

205

206 *Human-predator relations data*

207 Between May and September 2013 the questionnaire (Appendix S2 in supplementary information)
208 was administered face-to-face by NG who is Chilean and had no previous interaction with
209 respondents. All SUs contained residential properties and one or two households closest to the
210 camera-trap locations were surveyed (mean number of households per km^2 across the study
211 landscape: 3.4; range: 1.4 to 5.1 from INE 2002). For each household, the family member deemed to
212 be most knowledgeable with respect to farm management and decision-making was surveyed. The
213 questionnaire gathered data on socio-demographic/economic background, guiña encounters, livestock
214 ownership, frequency of livestock predation by guiñas and ownership of dogs on the land parcel. To
215 measure tolerance to livestock predation, participants were asked how they would respond to different
216 scenarios of livestock loss (mortality of 2, 10, 25, 50, >50 animals), with one possible option
217 explicitly stating that they would kill guiña. These data were also used as predictors of killing
218 behaviour in the RRT analysis (see below). The questionnaire was piloted with 10 local householders
219 living outside the SUs; their feedback was used to improve the wording, order and time scale of
220 predation and encounter questions.

221

The potential occupancy model predictors (Table 1, Appendix S2 & Table S1) were calculated per SU. Where questionnaire responses differed within a SU (e.g. one household report predation and the other did not), presence of the event (e.g. predation) was used as a covariate for that particular SU. For all quantitative measures, and when both respondents report the event (e.g. frequency of predation) median values were used.

Illegal killing prevalence across the landscape (other evidence)

As it is illegal to kill guiñas in Chile (Law 19.473 Ministry of Agriculture), the randomised response technique (RRT) (Nuno & St. John 2015) was used to ask this sensitive question as part of the questionnaire (Appendix S2). Since RRT, like other methods for asking sensitive questions, require a large sample size for precise estimation of behaviour prevalence (Nuno & St. John 2015), we pooled RRT data from all participants to estimate the prevalence of illegal guiña killing across the landscape over the past decade. We explored predictors that might explain this human behaviour (St John *et al.* 2012).

RRT data were bootstrapped 1000 times to obtain a 95% confidence interval. We tested seven non-correlated predictors of illegal guiña killing: age, income, frequency of guiña encounters, number of chickens owned (all continuous variables standardized to z-scores), economic dependency on their land parcel (1=no dependency; 2=partially dependency; 3=complete dependency), knowledge of the guiña's legal protection status (0=hunting prohibited; 1=do not know; 2=hunting permitted), and intention to kill a guiña under a hypothetical predation scenario (0=do nothing; 1=manage guiña; 2=kill guiña) (Appendix S2). We used R (version 3.2.3; R Core Team, 2014) to run the RRlog function of the package RRreg (version 0.5.0; Heck & Moshagen 2016) to conduct a multivariate logistic regression using the model for 'forced response' RRT data. We fitted a logistic regression model with the potential predictors of killing behaviour and evaluated their significance with likelihood ratio tests (LRT ΔG^2). Odds ratios and their confidence values are presented for model covariates.

250 ***Integrated socio-ecological modelling***

251 First, we evaluated the existence of spatial autocorrelation with detection/non-detection data for each
252 SU, using Moran's *I* index based on similarity between points (Dormann *et al.* 2007). We used a fixed
253 band distance of 3 km from the midpoint of camera-traps, equating to an area three times larger than a
254 guiña home range.
255
256 We fitted models of occupancy dynamics (MacKenzie *et al.* 2003) using PRESENCE, which obtains
257 maximum-likelihood estimates via numerical optimisation (Hines 2006). The probabilities of initial
258 occupancy (ψ), colonisation (γ), local extinction (ε) and detection sites (p) were used as model
259 parameters. We conducted a preliminary investigation to assess whether a base model structure with
260 Markovian dependence was more appropriate for describing seasonal dynamics, rather than assuming
261 no occupancy changes occur or that changes happen at random (MacKenzie *et al.* 2006). Once the
262 best model structure had been determined, we then fitted models with habitat configuration/quality
263 and human-predator predictors.
264
265 A total of 15 potential model predictors were tested for collinearity and, in instances where variables
266 were correlated (Pearson's/Spearman's $|r|>0.7$), we retained the covariate that conferred greater
267 ecological/social meaning and ease of interpretation (Table 1). All continuous variables, except
268 percentages, were standardized to z-scores. We approached model selection by increasing model
269 complexity gradually, fitting predictors for each model parameter separately and assessing model
270 performance using Akaike's Information Criterion (AIC). Models that were within <2 ΔAIC were
271 considered to have substantial support (Burnham & Anderson 2002), and thus these predictors were
272 selected and used in the next step in a forward manner (e.g. Kéry, Guillera-Arroita & Lahoz-Monfort
273 2013). To prevent over fitting (Burnham & Anderson 2002), we kept models with only one predictor
274 per parameter, with the exception of one model which evaluated the additive effect of shrub and forest
275 cover (shrub is a marginal habitat for the study species; Dunstone *et al.* 2002).
276

A set of detection models were fitted using the best base structure. Subsequently, we evaluated models that included habitat configuration/quality and human-predator relations data to test its effect on initial occupancy (ψ_1), while keeping colonisation and extinction specific. The best initial occupancy and detection models were then used to add further complexity to the colonisation and extinction components. We fitted all predictors for extinction. However, we assume that colonisation between seasons is primarily influenced by habitat configuration/quality variables, rather than human-predator relations. To explore the candidate model space, we worked on the structure for extinction probability followed by colonisation, and then repeated the process vice versa (Kéry, Guillera□Arroita & Lahoz□Monfort 2013). A constant or null model was included in all candidate model sets. Models with convergence problems or implausible parameter estimates (i.e. very large estimates and standard errors) were eliminated from each set.

Goodness of fit was evaluated by bootstrapping 5000 iterations (MacKenzie and Bailey 2004) in the R package AICcmodavg. This test provides a model fit statistic based on consideration of the data from all seasons at once (*P*-Global), as well as separate statistics for each season. We used the predict function in R package unmarked (Fiske & Chandler 2011) to produce plots of estimated relationships with the predictors and derive estimates of occupancy for each of the seasons.

All aspects of this project were approved by the School of Anthropology and Conservation Research and Research Ethics Committee, University of Kent, as well as the Villarrica Campus Committee of the Pontificia Universidad Católica de Chile.

Results

Habitat configuration/quality data

We excluded four habitat configuration/quality predictors due to collinearity with extent of forest cover and number of patches (Tables 1 & S1). Across the landscape, variation in the degree of habitat loss and fragmentation was substantial. Extent of forest cover in SU's ranged from 1.8% to 76% (mean=27.5%; SD=18.9), and shrub cover followed a similar pattern (range: 9.1% to 53.1%;

mean=26%; SD=8.3). The number of habitat patches per SU varied between 14 and 163 (mean=52.9; SD=25.7), and patch shape was diverse (index range: 1.3 (highly irregular forms) to 7.8 (regular forms); mean=3.13; SD=1.3). Some SUs included a relatively high length of edge (~48,000 m), whereas others had as little as 4,755 m.

Human-predator relations data and illegal killing prevalence across the landscape

A total of 233 respondents completed the questionnaire, of which 20% were women and 80% men. The median age of respondents was 55 years (interquartile range: 46 to 67). The participants had lived in their properties for 25 to 50 years (median=35), which varied from 1-1,200 ha in size (median=29). Land subdivision within SUs also varied widely from 1 to 314 properties (mean=41.3; SD=37.2). Respondents, on average, received a monthly income equivalent to US$558 (SD=2.81) and had completed 10 years of formal schooling.

Encounters with guiñas were rare. Nearly half of the respondents (49%, n=116) reported seeing a guiña during their lifetime. However, on average, the sighting occurred 17 years ago (SD=15). This percentage dropped to 10% and 21% during the last four (within the timeframe of the camera-trap survey) and 10 years (time period for the RRT question) respectively. Predation events were also uncommon. Only 16% of respondents (n=37) attributed a livestock predation event in their lifetime to a guiña, with just 7% (n=16) stating that this had occurred in the past decade. Of the guiña predation events over the past decade (n=16), 81% were recorded in Andean SUs.

When presented with scenario-style questions concerning hypothetical livestock predation by a guiña, 38% (n=89) of respondents stated that they would kill the felid if two chickens were lost, rising to 60% (n=140) if 25 chickens were attacked. Using RRT, we found that 10% of respondents admitted to having killed a guiña in the last 10 years (SE=0.09; 95% CI=0.02-0.18). The likelihood of a respondent admitting to killing guiña increased significantly with encounter frequency (β=0.85, SE=0.50; LRT ΔG^2 =4.18, p=0.04); those reporting the highest level of encounter rate were 2.34 times more likely to have killed the species compared to those not encountering guiña (Table 2). Data from

333 the scenario-based question on predation was excluded from the model due to a high β coefficient and
334 associated standard error.
335
336 ***Detection/non-detection data***
337 A total of 23,373 camera-trap days returned 713 sampling occasions with a guiña detection (season
338 1=96; season 2=185; season 3=240; season 4=192). The naïve occupancy estimate (i.e. proportion of
339 sites with detection) was similar across all four seasons (0.54; 0.52; 0.58; 0.59) and between the
340 central valley and Andean SUs (both areas >0.5). There was no evidence of spatial autocorrelation
341 among SUs during any survey season (season 1 Moran's I=-0.03 (α=0.74); season 2 I=0.05 (α=0.31);
342 season 3 I=0.05 (α=0.36); season 4 I=0.07 (α=0.17)).
343
344 ***Integrated socio-ecological multi-season occupancy modelling***
345 Our preliminary evaluation indicated that a model structure with Markovian dependence was an
346 appropriate description of the data. This dependence implies that guiña presence at a given site in a
347 particular season is dependent on whether that site was occupied in the previous season (Table 3).
348 Model 1.1 was chosen as the base structure for the modelling procedure because: (i) it is supported by
349 AIC; and, (ii) its parameterisation using extinction and colonisation (i.e. not derived parameters)
350 allowed the role of different potential predictors to be tested on these population processes. Also,
351 letting extinction and colonisation be season-specific accommodated for unequal time intervals
352 between sampling seasons.
353
354 Model selection for detection (models 2.1-2.7; Table 4) revealed a positive relationship with
355 understory vegetation cover (β_1 0.343; SE=0.055; Fig. 3b). There was no evidence of an effect
356 associated with the rotational camera-trap survey design, and none of the other predictors were
357 substantiated. Forest cover best explained initial occupancy (models 3.0-3.6; Table 4), with initial
358 occupancy being higher in sites with less forest cover, although the estimated relationship was weak
359 (β_1 =-0.0363; SE=0.0138; Fig. 3a). Adding shrub cover only improved model fit marginally.
360 Fragmentation metrics and land subdivision were not supported as good predictors.

361

362 Model selection for extinction and colonisation (models 4.0-4.18 and 5.0-5.12; Table 4) reflected the
363 same trends, irrespective of the order in which parameters were considered. Extinction, rather than
364 colonisation, yielded predictors that improved model fit compared to the null model. Where predictors
365 were fitted first on colonisation (models 5.0-5.5), none of the models tested improved fit substantially
366 compared to the null model. This indicated that, of the available predictors, colonisation was only
367 explained by seasonal differences. The human-predator predictors were not supported as drivers of
368 either initial occupancy or extinction probability (Table 4).

369

370 We fitted a final model (model 5.6; Table 4) with number of patches and land subdivision, which
371 were identified as important predictors in the two top competing extinction models (models 5.7 and
372 5.8). This model was well supported. A goodness-of-fit test suggested lack of fit based on the global
373 metric (P-global<0.05), but inspection of survey-specific results show no such evidence (p>0.05)
374 apart from season 2 (p=0.032). Inspecting the season 2 data, we found that the relatively large statistic
375 value appeared to be driven by just a few sites with unlikely capture histories (i.e. <12 detections).
376 Given this, and the fact that data from the other seasons do not show lack of fit, we deem that the final
377 model explains the data appropriately. The model predicts that SU extinction probability becomes
378 high (>0.6) when there are less than 27 habitat patches, and more than 116 land subdivisions (β_1 =-
379 0.900; SE=0.451 and β_1 =0.944; SE=0.373 respectively; Figs. 3c, d). Occupancy estimates were high
380 across seasons with derived seasonal estimates of 0.78 (SE=0.09), 0.64 (SE=0.06), 0.80 (SE=0.06)
381 and 0.83 (SE=0.06).

382

383 **Discussion**

384 The integrated socio-ecological multi-season occupancy modelling framework we present here
385 provides important insights into how habitat configuration/quality and human-predator relations may
386 interact in space and time to effect carnivore populations existing across a human-dominated
387 landscape. We were able to disentangle the relative impact of a range of threats that have been

388 highlighted previously in the literature as potential drivers of decline for our case study species the
389 guiña.
390
391 The guiña is an elusive forest specialist. As such, one might predict that the species would be highly
392 susceptible to both habitat loss and fragmentation (Henle *et al.* 2004b; Ewers & Didham 2006). While
393 the relationship between occupancy and higher levels of forest cover (Fig. 3a) does suggest guiñas are
394 likely to occupy areas with a large spatial extent of available habitat, our results also indicate that the
395 species can tolerate extensive habitat loss. The effects of habitat loss could be confounded by time,
396 and it is possible that we are not yet observing the impacts of this ecological process (Ewers &
397 Didham 2006). However, this is unlikely to be the case in this landscape as over 67% of the original
398 forest cover was lost by 1970 and, since then, deforestation rates have been low (Miranda *et al.* 2015).
399 Indeed, the findings highlight that intensive agricultural landscapes are very relevant for guiña
400 conservation and should not be dismissed as unsuitable.
401
402 Spatially, the occupancy dynamics of this carnivore appear to be affected by fragmentation and
403 human pressure through land subdivision. Ensuring that remnant habitat patches are retained in the
404 landscape, and land subdivision is reduced so that existing bigger farms are preserved, could
405 ultimately safeguard the long-term survival of this threatened species. This should be the focus of
406 conservation efforts, rather than just increasing the extent of habitat. Our findings further suggest that
407 these remnant patches may play a key role in supporting the guiña in areas where there has been
408 substantial habitat loss and, perhaps, might even offset local extinctions associated with habitat cover
409 (Fahrig 2002). A land sharing scheme within agricultural areas of the landscape could prove to be a
410 highly effective conservation strategy (Phalan *et al.* 2011) considering that these farms are currently
411 not setting aside land, but are of high value to the species. The results also highlight that farmers with
412 large properties are key stakeholders in the conservation of this species and must be at the centre of
413 any conservation interventions that aim to protect existing native forest vegetation within farmland.
414

Following farming trends globally, larger properties in the agricultural areas of southern Chile are generally associated with high intensity production, whereas smaller farms are mainly subsistence-based systems (Carmona *et al.* 2010). It is therefore interesting, but perhaps counterintuitive, that we found occupancy to be higher (lower local extinction) where there is less land subdivision. However, a greater number of small farms is associated with higher human density which may result in increased persecution by humans (Woodroffe 2000). Also, higher subdivision imposes pressure on natural resources, due to more households being present in the landscape (e.g. Liu *et al.* 2003), which has been shown to reduce the quality of remaining habitat patches as a result of frequent timber extraction, livestock grazing (Carmona *et al.* 2010) and competition/interference by domestic animals and pets (Sepúlveda *et al.* 2014). Native vegetation in non-productive areas, including ravines or undrainable soils with a high water table, is normally spared within agricultural areas (Miranda *et al.* 2015), and these patches of remnant forest could provide adequate refuge, food resources and suitable conditions for carnivore reproduction (e.g. Schadt *et al.* 2002). However, it is possible that areas with high land subdivision and a large number of patches could be acting as ecological traps if source-sink dynamics are operating in the landscape (Robertson & Hutto 2006). Additionally, another factor driving the subdivision of land and degradation of remnant forest patches across agricultural areas is the growing demand for residential properties (Petitpas *et al.* 2017). This is facilitated by Chilean law, which permits agricultural land to be subdivided to a minimum plot size of 0.5 ha. Furthermore, it is common practice for sellers and buyers to completely eliminate all understory vegetation from such plots (C. Rios, personal communication) which, as demonstrated by detection being higher in dense understory, is a key component of habitat quality. The fact that farmers to subdivide their land for economic profit, driven by demand for residential properties, is a very complex and difficult issue for future landscape-level conservation.

Although previous studies have suggested that human persecution may be a factor contributing to the decline of the guiña (Nowell & Jackson 1996; Sanderson, Sunquist & W. Iriarte 2002), illegal killing in the study region appears low and much less of a threat to the species than the habitat configuration in the landscape. Despite the fact that the species occupies a large proportion of the landscape across

443 seasons, people report that they rarely encounter the carnivore or suffer poultry predation. The guiña's
444 elusive behaviour is reinforced by our low camera-trap detection probability (p<0.2 over 2 nights).
445 One in ten respondents (10%) admitted to killing a guiña over the last decade. One potential drawback
446 of RRT is that it is impossible to know if people are following the instructions (Lensvelt-Mulders &
447 Boeije 2007). However, we deployed a symmetrical RRT design (both 'yes' and 'no' were assigned
448 as prescribed answers), which increases the extent to which people follow the instructions (Ostapczuk
449 & Musch 2011). Moreover, the proportion of 'yes' answers in the data exceeded the probability of
450 being forced to say 'yes' (which in this study was 0.167), indicating that respondents were reporting
451 illegal behaviour.
452
453 Identification of individual guiñas from camera-trap images is unfeasible (F. Blair unpublished data),
454 meaning that it is not currently possible to estimate robustly changes in abundance through time or
455 conduct population viability analyses, which is true for many unmarked animals (MacKenzie *et al.*
456 2006; MacKenzie & Reardon 2013). Consequently, it could be difficult to determine whether a certain
457 prevalence of illegal killing is having a detrimental impact on the population size of the species.
458 However, with our framework we could, in the future, evaluate spatial layers of information such as
459 the probability of illegal killing based on the distribution of encounters with the guiña and landscape
460 attributes that increase extinction probability (e.g. land subdivision and reduced habitat patches) in
461 order to be spatially explicit about where to focus conservation and research efforts (e.g. Santangeli *et*
462 *al.* 2016).
463
464 Our results demonstrate the benefits of integrating socio-ecological data into a single modelling
465 framework to gain a more systematic understanding of the drivers of species decline. Research and
466 conservation plans of several small to medium carnivores could benefit from such a framework
467 (Brooke *et al.* 2014). It could tease apart the relative importance of different threats, such as for our
468 study species, in order to make informed recommendations as to the type of conservation efforts that
469 should be prioritised. Better links between social and natural sciences are needed (Redpath *et al.*

2013; Pooley *et al.* 2016). Our framework can contribute to this aim for a range of species and social contexts within human-dominated landscapes.

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Figure Legends

Figure 1: Integrated socio-ecological multi-season occupancy modelling framework to assess drivers of carnivore decline in a human-dominated landscape.

Figure 2: Distribution of landcover classes and protected areas across the study landscape in southern Chile, including the forest habitat of our case study species, the guiña (*Leopardus guigna*). The two zones within which the 145 sample units (SU: 4 km^2) were located are indicated, with 73 SUs in the central valley (left polygon) and 72 within the Andes (right polygon). Illustrative examples of the variation in habitat configuration within SUs across the human-domination gradient are provided (bottom of image).

Figure 3: Predicted effects of forest cover, understory density, number of habitat patches and land subdivision on multi-season occupancy model parameters for the guiña (*Leopardus guigna*). These results correspond to the final selected model [ψ_1(Forest), *p*(season+Understory), ε(season+PatchNo+Subdivision), γ(season)]. Grey lines delimit 95% confidence intervals.

678 **Table 1:** Habitat configuration/quality and human relation predictors evaluated when modelling initial
679 occupancy (ψ_1), colonisation (γ), extinction (ε) and detection (p) probability parameters of multi-
680 season camera-trap guiña (*Leopardus guigna*) surveys. Further details can be found in Appendix S1,
681 S2 & Table S1.
682

Parameter	Predictor	Abbreviation in models
	Habitat configuration	
ψ_1, ε, γ	Percent of forest cover/habitat[†]	Forest
ψ_1, ε, γ	Percent shrub cover/marginal habitat	Shrub
ψ_1, ε, γ	Number of forest patches	PatchNo
ψ_1, ε, γ	Shape index forest patches	PatchShape
ψ_1, ε, γ	Forest patch size area[‡]	PatchAreaW
ψ_1, ε, γ	Forest patch continuity[‡]	Gyration
ψ_1, ε, γ	Edge length of forest land cover class	Edge
ψ_1, ε, γ	Landscape shape index of forest[§]	LSI
ψ_1, ε, γ	Patch cohesion[‡]	COH
	Human predator relations	
ψ_1, ε	Land subdivision	Subdivision
ψ_1, ε	Intent to kill (hypothetical scenario questions)	Intent
ψ_1, ε	Predation	Predation
ψ_1, ε	Frequency of predation	FQPredation
ψ_1, ε, p	Frequency of encounter[††]	FQEncounter
ψ_1, ε	Number of dogs	Dogs
	Habitat quality	
p	Bamboo density (*Chusquea* spp.)	Bamboo
p	Density of understory	Understory
p	Sample Unit rotation block	Rotation
p	Intensity of livestock activity	Livestock
p	Intensity of logging activity	Logging
p	Water availability	Water

683 [†]Pools together all forest types: old-growth, secondary growth, and wetland forest
684 [‡] Predictor excluded due to collinearity with percent of forest cover (Pearson's $|r|>0.7$)
685 [§] Predictor excluded due to collinearity with number of forest patches (Pearson's $|r|>0.7$)
686 [††] Predictor also fitted with detection probability
687
688
689

690 **Table 2:** The relationship between illegal killing of guiña (*Leopardus guigna*) and potential predictors
691 of the behaviour. Reported coefficients, standard errors, odds ratios and their 95% confidence
692 intervals were derived from a multivariate logistic regression which incorporates the known
693 probabilities of the forced RRT responses. Significance was accepted at the 0.05 level.
694

					Odds ratio	
	Coefficient	**SE**	***p***	**Odds ratio**	**Lower CI**	**Upper CI**
(Intercept)	-2.43	1.99	0.25	0.09	0.00	4.36
Age	-0.41	0.43	0.38	0.66	0.29	1.54
Income	0.00	0.55	0.99	0.99	0.34	2.96
Land parcel dependency	0.02	0.83	0.98	12.02	0.20	5.19
Number of chicken holdings	-0.18	0.71	0.78	0.83	0.21	3.38
Knowledge of legal protection	0.48	0.77	0.57	1.62	0.36	7.37
Frequency of encounter	0.85	0.50	0.04	2.34	0.87	6.28

695

696

Table 3: Seasonal occupancy dynamics models following MacKenzie et. al. (2006), applied to the guiña (*Leopardus guigna*), to define the base model structure for the subsequent model selection procedure to evaluate potential habitat configuration/quality and human-predator predictors. Fitted probability parameters are occupancy (ψ), colonisation (γ), extinction (ε) and detection (p). Models assess whether changes in occupancy do not occur (model 1.6), occur at random (models 1.5, 1.4) or follow a Markov Chain process (i.e. site occupancy status in a season is dependent on the previous season) (models 1.0, 1.1, 1.2, 1.3). Initial occupancy (ψ_1) refers to occupancy in the first of four seasons over which the guiña was surveyed. Model selection procedure is based on Akaike's Information Criterion (AIC). ΔAIC is the difference in AIC benchmarked against the best model, w_i is the model weight, K the number of parameters, and -2*loglike is the value of the log likelihood at its maximum. The selected model is highlighted in bold.

Model	Seasonal dynamic models	ΔAIC	w_i	K	-2*loglike
1.0	$\psi(.)$, $\gamma(.)$, $\{\varepsilon = \gamma\ (1-\psi)/\psi\}$, p(season)	0.00	0.443	6	3982.93
1.1	**$\psi_1(.)$, ε(season), γ(season), p(season)**	**0.36**	**0.370**	**11**	**3973.29**
1.2	$\psi_1(.)$, $\varepsilon(.)$, $\gamma(.)$, p(season)	1.88	0.173	7	3982.81
1.3	$\psi_1(.)$, $\varepsilon(.)$, $\gamma(.)$, $p(.)$	6.83	0.015	4	3993.76
1.4	$\psi_1(.)$, $\gamma(.)$,$\{\varepsilon = 1-\gamma\}$, p(season)	41.78	0.000	6	4024.71
1.5	$\psi_1(.)$, γ(season),$\{\varepsilon = 1-\gamma\}$, p(season)	42.78	0.000	8	4021.71
1.6	$\psi(.)$, $\{\gamma = \varepsilon = 0\}$, p(season)	104.11	0.000	6	4087.04

712 **Table 4:** Multi-season models of initial occupancy (ψ_1), extinction (ε), colonisation (γ) and detection
713 (p) probability with potential habitat configuration/quality and human-predator predictors for the
714 guiña (*Leopardus guigna*). Predictors were evaluated with a base model of seasonal dynamics [ψ_1(.),
715 ε(season), γ(season), p(season)] using a step-forward model selection procedure and Akaike's
716 Information Criterion (AIC). Initial occupancy (ψ_1) refers to occupancy in the first of four seasons
717 over which the guiña was surveyed, with occupancy dynamics following a Markov Chain process.
718 ΔAIC is the difference in AIC benchmarked against the best model, w_i is the model weight, K the
719 number of parameters, and -2*loglike is the value of the log likelihood at its maximum. The selected
720 models for each parameter are highlighted in bold and used in the next step. ε was fitted first followed
721 by γ, then vice versa.

Model	Fitted parameter	ΔAIC	w_i	K	-2*loglike
	Detection/fitted with ψ_1(.), ε(season), γ(season)				
2.0	***p*(season+Understory)**	**0.00**	**0.9999**	**12**	**3934.47**
2.1	*p*(season+Bamboo)	18.48	0.0001	12	3952.95
	Initial occupancy/fitted with ε(season), γ(season), p(season+Understory)				
3.0	**ψ_1(Forest)**	**0.00**	**0.5425**	**13**	**3927.46**
3.1	ψ_1(Forest+Shrub)	1.24	0.2918	14	3926.7
3.4	ψ_1(PatchNo)	4.00	0.0734	13	3931.46
3.5	ψ_1(.)	5.01	0.0443	12	3934.47
3.6	ψ_1(Subdivision)	5.69	0.0315	13	3933.15
3.7	ψ_1(Dogs)	7.00	0.0164	13	3934.46
	Extinction first/fitted with ψ_1(Forest), p(season+Understory)				
4.0	**ε(season+PatchNo), γ(season)**	**0.00**	**0.4692**	**14**	**3920.10**
4.1	**ε(season+Subdivision), γ(season)**	**0.36**	**0.3919**	**14**	**3920.46**
4.2	ε(season+PatchShape), γ(season)	5.15	0.0357	14	3925.25
4.3	ε(season+Predation), γ(season)	5.24	0.0342	14	3925.34
4.4	ε(season), γ(season)	5.36	0.0322	13	3927.46
4.5	ε(season+FQencounter), γ(season)	5.92	0.0243	14	3926.02
4.6	ε(season+FQPredation), γ(season)	7.24	0.0126	14	3927.34

	Colonisation second/fitted with ψ_1(Forest), p(season+Understory) and 4.0/4.1 for ε				
4.7	**ε(season+PatchNo), γ(season)**	**0.00**	**0.1877**	**14**	**3920.10**
4.8	**ε(season+Subdivision), γ(season)**	**0.36**	**0.1568**	**14**	**3920.46**
4.9	ε(season+Subdivision), γ(season+PatchShape)	0.79	0.1265	15	3918.89
4.10	ε(season+PatchNo), γ(season+PatchShape)	1.29	0.0985	15	3919.39
4.11	ε(season+Subdivision), γ(season+PatchNo)	1.63	0.0831	15	3919.73
4.12	ε(season+PatchNo), γ(season+Edge)	1.84	0.0748	15	3919.94
4.13	ε(season+PatchNo), γ(season+Forest)	1.98	0.0698	15	3920.08
4.14	ε(season+Subdivision), γ(season+Edge)	2.16	0.0638	15	3920.26
4.15	ε(season+ Subdivision), γ(season+Forest)	2.20	0.0625	15	3920.30
4.16	ε(season+Subdivision), γ(season+Forest+Shrub)	3.50	0.0326	16	3919.60
4.17	ε(season+PatchNo), γ(season+Forest+Shrub)	3.60	0.0310	16	3919.70
4.18	ε(season), γ(season)	5.36	0.0129	13	3927.46
	Colonisation first/fitted with ψ_1(Forest), p(season+Understory)				
5.0	**ε(season), γ(season)**	**0.00**	**0.3303**	**13**	**3927.46**
5.1	ε(season), γ(season+PatchShape)	0.96	0.2044	14	3926.42
5.2	ε(season), γ(season+PatchNo)	1.55	0.1522	14	3927.01
5.3	ε(season), γ(season+Edge)	1.89	0.1284	14	3927.35
5.4	ε(season), γ(season+Forest)	1.95	0.1246	14	3927.41
5.5	ε(season), γ(season+Forest+Shrub)	3.41	0.06	15	3926.87
	Extinction second/fitted with ψ_1(Forest), p(season+Understory) γ(season)				
5.6	**ε(season+PatchNo+Subdivision), γ(season)**	**0.00**	**0.8275**	**15**	**3913.45**
5.7	ε(season+PatchNo), γ(season)	4.65	0.0809	14	3920.10
5.8	ε(season+Subdivision), γ(season)	5.01	0.0676	14	3920.46
5.9	ε(season+PatchShape), γ(season)	9.80	0.0062	14	3925.25
5.10	ε(season+Predation), γ(season)	9.89	0.0059	14	3925.34
5.11	ε(season), γ(season)	10.01	0.0055	13	3927.46
5.12	ε(season+FQEncounters), γ(season)	10.57	0.0042	14	3926.02
5.13	ε(season+FQPredation), γ(season)	11.89	0.0022	14	3927.34

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Supporting Information

Appendix S1: Landcover classification of study area

Landcover classification was carried out using a composite of four Aster images at 15 m resolution from between 2002 and 2007. Native forest cover within the study region did not change significantly between 1983 and 2007 (Petitpas 2010; Miranda *et al.* 2015). In addition, the current extent and configuration of forest across the sample units (SUs) has not altered perceptibly when compared visually with up-to-date Google Earth imagery from 2014. The study region was categorised into nine landcover classes ((i) water; (ii) forest, (iii) forest regrowth, (iv) shrub/bog, (v) grassland, (vi) hualve (inundated forests), (vii) plantation, (viii) crop/pasture/orchard and (ix) bare ground/sand/lava rock) using a supervised classification with maximum likelihood estimation, based on field data from 738 training points. A further 738 points were used to verify classification accuracy, which was 'almost perfect' (Kappa= 0.81 (SE= 0.017); Landis & Koch 1977; Congalton 1991). Urban landcover digitised by hand and added as a tenth class. Image processing and classification were conducted in ERDAS Imagine 2014 (Hexagon Geospatial, Norcross, GA, USA) and ArcMap v.10.1 (ESRI, Redlands, CA, USA).

742 **Appendix S2: Generation of the human-predator relations data, used as potential predictors to**
743 **model multi-season occupancy dynamics of the guiña (*Leopardus guigna*)**

744 The questionnaire delivery and design were approved by School of Anthropology and Conservation
745 Research and Research Ethics Committee, University of Kent, as well as the Villarrica Campus
746 Committee of the Pontificia Universidad Católica de Chile. All householders were fully informed of
747 the study objectives, but with care taken to ensure that the information provided would not lead to
748 (un)conscious bias in the participant's responses. The contact and employment details for the
749 principal researcher were provided in case any unforeseen issues were experienced after completing
750 the questionnaire. The respondents were told that their engagement in the research was entirely
751 voluntary and that they could withdraw from the process at any point, without needing to provide an
752 explanation. Additionally, they were notified that their answers to the questionnaire would be
753 anonymised and only ever presented in aggregate form, so their identity would not be discernible. The
754 respondents were also assured that the data would be stored securely, only accessible by the lead
755 researcher and would not be passed on to any second parties, in line with the UK Data Protection Act.
756 Each individual was then given time to evaluate all this information, prior to signing an informed
757 consent sheet.
758
759 The questionnaire consisted of six sections. The first part included socio-demographic/economic
760 questions relating to age, amount of schooling, livelihood activities and income. The next section
761 focussed on questions regarding killing wild animals, including species with protected (e.g. puma,
762 guiña) and non-protected status (e.g. introduced wild boar). To prevent any bias in responses, our
763 questions included all native carnivores known to occur across the study region, as well as free-
764 roaming domestic dogs. As killing of protected species is an illegal activity, we employed the
765 Randomised Response Technique (RRT) described in St John et al. (2010). A dice was used as
766 randomisation tool; respondents were asked to provide a truthful answer if they rolled a one, two,
767 three or four, must answer "yes" if they rolled a five (irrespective if it is true answer or not) and must
768 answer "no" if the dice landed on six. The time period used to provide context to the question was
769 'over the last ten years', which was deemed most appropriate after the pilot exercise. Trial runs were

conducted using non-sensitive questions to ensure the RRT instructions were understood and being followed by the respondents. A visual barrier was used to ensure that the interviewer could not see the number on the rolled dice.

The third part of the questionnaire asked respondents to report livestock losses via predation over the past year, or an alternative time period they could quantify. In the fourth section, participants were probed about their knowledge of whether the hunting of each species was permitted or illegal, as well as asking how frequently the species were encountered. A fifth section aimed to evaluate scenarios of predation with a hypothetical livestock holding of 100 sheep and chickens. Respondents were asked what behaviour they would display towards the carnivores occurring in the study region after a specific level of predation (2, 10, 25, 50, >50 sheep or chickens) has been experience. For sheep predation, we assessed the puma (*Puma concolor*) and domestic dogs (*Canis familiaris*), and for chicken predation we asked about guiña and Harris hawk (*Parabuteo unicinctus*). In order not to bias responses, respondents were offered a choice of possible actions (e.g. lethal controls, call authorities, improve management, nothing, etc.). The value of this hypothetical predation scenario was interpreted as a measure to tolerance to predation. The final section centred on the management of livestock, particularly sheep and chickens, in relation to behaviour such as enclosing livestock at night, the distance of the closure from household, the number of domestic dogs/cats associated with the property and how they are managed overnight (e.g. free-roaming, tethered), as well as how often they are fed and the type of food they are given.

791 The original (Spanish) and translated (English) questions were as follows:

RANDOMISED RESPONSE (RRT)	Response Type
1. During the last 10 years, have you killed a wildboar? En los últimos diez años ha matado a un Jabalí?	Yes/No
2. During the last 10 years, have you killed a puma? En los últimos diez años ha matado a un puma?	Yes/No
3. During the last 10 years, have hired someone to kill a puma? En los últimos diez años ha matado a contratado a alguien para matar a un puma?	Yes/No
4. During the last 10 years, have you killed a guiña? En los últimos diez años ha matado a una guiña?	Yes/No
5. During the last 10 years, have you killed a fox? En los últimos diez años ha matado a un zorro?	Yes/No
6. During the last 10 years, have you killed a hawk? En los últimos diez años ha matado a un peuco?	Yes/No
7. During the last 10 years, have you killed a rabbit or hare? En los últimos diez años ha matado a un conejo o liebre?	Yes/No
8. During the last 10 years, have you killed a free roaming domestic dog not of your ownership? En los últimos diez años ha matado a un perro doméstico andariego que no es de su propiedad?	Yes/No
9. During the last 10 years, have you killed a weasel? En los últimos diez años ha matado a un quique?	Yes/No
10. During the last 10 years, have you killed a skunk? En los últimos diez años ha matado a un chingue?	Yes/No
HOUSEHOLD INFORMATION	
11. What is the size of your property in hectares? Cuál es el tamaño de su propiedad?	*Exact figure*
12. How long have you lived here? Where are you originally from? Hace cuánto vive en el sector? De donde es?	*Exact figure*
13. What is your age? And that of other adults in the household? Cuál es la edad de los adultos del hogar? (dueños de casa)	*Exact figure*
14. What is your level of schooling? And that of other adults in the household? Cuál es el nivel escolar de los adultos del hogar? (dueños de casa)	*Exact figure*
15. How many children do you have? Cuantos hijos tiene?	*Exact figure*
16. Please classify in order of importance the following economic activities for your overall income? Clasifique en orden de importancia para su ingreso familiar las siguientes actividades económicas?	Crops/Livestock/Forestry/Urban services/ Agricultural services/Tourism/Subdivision of

	land for residential development/Other
17. What is your approximate monthly income? Cuál es su ingreso mensual aproximado?	*Exact figure*
PREDATION OF DOMESTIC ANIMALS	
18. What are your livestock animal holdings during the past year? Cuantos animales ha tenido durante el año pasado?	Bovine/Ovine/Chickens/Others
19. How many livestock animals have you lost because of this predator in the past year? If respondent could not quantify over the past year their alternative time period was noted (e.g. 3 sheep killed by puma in 5 years) Cuántos animales ha perdido por parte del predador? Si el entrevistado no podía cuantificar en un año, entonces se anotaba el periodo de tiempo en el cual sufrió un numero de pérdida (e.g. 3 ovejas predadas por puma en 5 años) *The question was repeated in turn for the following predators: puma, guiña, fox, hawk, domestic dogs, skunk, weasel* *La pregunta fue repetida para puma, guiña, zorros, peucos (rapaces diurnas), perros domésticos, chingues y quique.*	*Exact figure*
KNOWLEDGE OF PREDATOR LEGAL STATUS	
20. From your knowledge, is hunting this predator prohibited? Según su conocimiento, se puede cazar al animal? *The question was repeated in turn for the following predators:* puma, guiña, fox, hawk, domestic dogs, skunk, weasel, hare-rabbit La pregunta fue repedita para puma, guiña, zorros, peucos (rapaces diurnas), perros domésticos, chingues, quique y liebre y conejos	Yes/No/Do not know
FREQUENCY OF PREDATOR ENCOUNTERS	
21. How frequently do you observe a sign or sound indicating that this predator has been on your property? Please use a unit of time that you can remember (daily, weekly, monthly, yearly) Con que frecuencia observa (o algún indicio) al animal en su propiedad? Use una medida de tiempo que recuerde (diario, semanal, mensual, anual). *The question was repeated in turn for the following predators:* puma, guiña, fox, hawk, domestic dogs, skunk, weasel, hare-rabbit La pregunta fue repedita para puma, guiña, zorros, peucos (rapaces diurnas), perros domésticos, chingues, quique y liebre y conejos	*Exact figure*
SCENARIO-BASED QUESTION: HYPOTHETICAL RESPONSE TO PREDATION	Open ended question with internal codes for: (1)Call authorities; (2)Intent to hunt it; (3)Capture and call authorities; (4)Scare off; (5)Nothing; (6)Observe; (7)Protect my livestock holdings; (8)other
"Let's suppose that you have 100 sheep" / "Digamos que usted tiene 100 ovejas"	
22. What do you think you would do if the puma kills X/100 Sheep Qué haría si un puma le mata X/100 ovejas? X = 2, 10, 25, 50, >50	Internal code

23. What do you think you would do if a domestic dog kills X/100 sheep Qué haría si un perro doméstico le mata X/100 ovejas? X = 2, 10, 25, 50, >50	Internal code
"Let's suppose that you have 100 Sheep" / "Digamos que usted tiene 100 Ovejas"	
24. What do you think you would do if the guiña kills X/100 chickens? Qué haría si un guiña le mata X/100 chickens? X = 2, 10, 25, 50, >50	Internal code
What do you think you would do if a hawk kills X/100 chickens? Qué haría si un peuco (todas las rapaces diurnas) le mata X/100 gallinas? X = 2, 10, 25, 50, >50	Internal code
DOMESTIC ANIMAL MANAGEMENT	
25. How do you keep your livestock animals at night? Como guarda sus animales durante la noche? Question asked for sheep and chickens Pregunta realizada para ovejas y gallinas	Closed housing/Open corral/Open field with dog/Open field without dog/Other, how?
26. At what distance do you keep your livestock animals at night? meters A que distancia de su casa guarda sus animales durante la noche? metros Question asked for sheep and chickens Pregunta realizada para ovejas y gallinas	*Exact figure*
27. How many dogs/cats do you have? Cuantos perros/gatos tienen en su casa?	*Exact figure*
28. What do you do with your dogs/cats at night? Que hace con sus perros/gatos durante la noche?	Enclosure/Tied/Free-roaming/Other
29. With what do you feed your dog/cat? Con que alimenta a sus perros/gatos?	Commercial pellets/Kitchen scraps/Mix of pellets and kitchen scraps/Grain/Mix of grain and kitchen scraps/Nothing/Other

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793

794 **Table S1:** Description of potential habitat configuration/quality and human-predator predictors used when modelling initial occupancy (ψ_1), colonisation (γ),
795 extinction (ε) and detection (p) probability parameters from multi-season camera-trap surveys of the guiña (*Leopardus guigna*). Detailed description of habitat
796 configuration metrics can be found in (McGarigal *et al.* 2002).

Predictor	**Abbreviation in models**	**Description**[§§]
Habitat configuration		
Percent forest cover	Forest	Metric that measures habitat loss as the extent of forest cover in a sample unit (0-100). Forest cover was obtained by pooling old-growth and secondary forest landcover classes, which are both considered to be suitable guiña habitat (Nowell & Jackson 1996; Acosta-Jamett & Simonetti 2004).
Percent shrub cover	Shrub	Metric that measures the extent of shrub cover in a sample unit (0-100). The spatial configuration is not assessed because shrub is a marginal habitat and evaluated for an additive effect on forest cover. As shrub can be considered a marginal habitat for guiña (Dunstone *et al.* 2002; Sanderson, Sunquist & W. Iriarte 2002; Acosta-Jamett & Simonetti 2004), we also measured the extent of shrub cover to evaluate possible additive effects with habitat cover
Number of forest patches	PatchNo	Metric that measures the number of forest habitat patches (0-∞).
Shape index forest patches	PatchShape	Shape metric that measures the complexity of forest habitat patch shape compared to a square, weighted for the entire landscape. As the index value increases, that habitat patch shape is more irregular (1-∞).
Forest patch size area[†]	PatchAreaW	Metric that measures mean habitat patch area (0-∞) corrected for sample unit scale. It provides a landscape centric perspective of patch structure.
Forest patch continuity[†]	Gyration	Metric that measures habitat patch continuity (0-∞). It can be interpreted as the average distance an organism can move within the habitat before an edge is encountered (McGarigal *et al.* 2002). The value increases with greater habitat patch extent.
Edge length of forest	Edge	Area-edge metric that measures the total length (0-∞) of habitat patch edge across a sample unit. This can be used instead of edge density because we are comparing sample units of the same size (McGarigal *et al.* 2002). The value rises with increasing edge.
Landscape shape index of forest[‡]	LSI	Aggregation metric that compares the landscape level edge of the habitat to one without internal edges or a square (0-100). This is a measure of the level of fragmentation in a sample unit.

Patch Cohesion[†]	COH	Aggregation metric that measures the physical connectedness (0-1) of forest habitat cover by measuring the aggregation of patches.
Human-predator relations data		
Land subdivision	Subdivision	Measures the number of land tenure divisions (i.e. owners) in a sample unit (0-∞). We expect higher subdivision to represent greater anthropogenic pressure and management variability from factors such as logging and presence of domestic dogs which were not measured directly in each sample unit (e.g. Theobald, Miller & Hobbs 1997; Hansen *et al.* 2005; Western, Groom & Worden 2009). Subdivision was based on the number of properties or land parcels recorded in each SU from national records (CIREN-CORFO, 1999).
Intent to kill	Intent	Intent to kill guiña by households in a sample unit (categorical: yes= 1, no= 0). This measure describes how a respondent states they would respond if a guiña two of their chickens. It is a highly conservative indicative measure of tolerance to livestock predation before lethal control is considered.
Predation	Predation	Occurrence of chicken predation by guiña in a sample unit (categorical: yes= 1, no= 0).
Frequency of predation	FQPredation	Frequency of chicken predation by guiña in a sample unit. Predation events were scaled to yearly frequency (0-∞).
Frequency of encounter[§]	FQEncounter	Numbers of encounters householders have had with guiña, scaled to a yearly frequency (0-∞). Frequency of encounters is also used to fit detection probability as a proxy for the elusiveness of the species.
Number of dogs	Dogs	Maximum number of free-roaming dogs, owned by the household, at night in proximity to the camera-traps (0-∞). We assume this value to be a conservative proxy to dog activity and an index of interference/competition by dogs. We also fitted extinction probability with free roaming dogs as they have been documented to interfere and kill wildlife in Chile (Silva-Rodriguez, Ortega-Solis & Jimenez 2010; Silva-Rodríguez & Sieving 2012), therefore we included average number of free roaming domestic dogs of nearby households (from our questionnaire Appendix S2 as a potential source of mortality. Because guiña are mainly nocturnal (Delibes-Mateos *et al.* 2014; Hernandez *et al.* 2015) we excluded households that restrain dogs at night.
Habitat quality and survey specific variables[§]		
Bamboo density (*Chusquea* spp.)	Bamboo	Bamboo density (*Chusquea* spp.) within a 25 m radius of each camera-trap, recorded in five categorical percentage classes (Braun-Blanquet 1965).

Density of understory	Understory	Understory vegetation density within a 25 m radius of each camera-trap, recorded in five categorical percentage classes (Braun-Blanquet 1965).
SU rotation	Rotation	Each SU was included in one of four consecutively sampled rotations of camera-traps during each season.
Intensity of livestock activity	Livestock	Livestock activity next to each camera-trap visually assessed and recorded using three categories (high, medium or low intensity). Based on signs such as presence of animals, grazed vegetation, trampled paths and manure.
Intensity of logging activity	Logging	Logging activity next to each camera-trap visually assessed and recorded using three categories (high, medium or low intensity). Based on signs such as active firewood piles, clearings, logging paths, fresh stumps and fallen logs.
Water availability	Water	The availability of water was recorded as either present or absent at the patch level during each season (categorical: yes= 1, no= 0).

797 [†]Predictor excluded due to collinearity with percent of forest cover (Pearson's $|r|>0.7$)

798 [‡]Predictor excluded due to collinearity with number of forest patches (Pearson's $|r|>0.7$)

799 [§]Predictors fitted only with detection probability at the forest patch level

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Integrating ecological and social data to assess drivers of carnivore decline within a human-dominated landscape

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Summary

1. Habitat loss and fragmentation, resulting from land-use change, are key threats to the long-term persistence of terrestrial mammals, particularly carnivores which are also susceptible to direct persecution by people. Carnivore conservation needs focussed interventions in human-dominated landscapes. An in-depth understanding of the ecological and social factors associated with species decline is thus needed in order to develop effective action plans.
2. We use a multi-season camera-trap occupancy modelling framework to assess the dynamics of a case study species, the threatened guiña (*Leopardus guigna*), over an extensive landscape representing an agricultural-use gradient. Data used in the modelling were derived from four seasons of camera-trap surveys, remote-sensed images and household questionnaires. Specifically, we examine how habitat loss, fragmentation and human pressures impact the species. Additionally, we estimate the prevalence and predictors of illegal guiña killing by householders across the study region, using the Random Response Technique.
3. The felid is elusive, with a low detection probability ($p<0.2$). Occupancy dynamics are supported by Markov chain processes, indicating that the occupancy status of the species in any given season depends on the previous one.
4. Guiña can tolerate a high degree of habitat loss, as long as the landscape is not overly subdivided into many farms and a high number of remnant habitat patches are retained. Illegal killing, livestock predation events and human encounters with the species are not likely to be driving local extinctions. However, farmers who have encountered guiña more frequently are increasingly likely to kill one.
5. *Synthesis and applications*. Human-dominated landscapes with large intensive farms can be of conservation value for elusive species, as long as an appropriate network of habitat patches exists. Despite human persecution being considered a key factor in the decline of many carnivores, including the guiña, we find that this is not the case in the study region. Our study demonstrates the value of taking an interdisciplinary approach to assessing the threats to a carnivorous mammal, by integrating ecological and social data into a single modelling framework. It has allowed us to tease apart the relative importance of different potential

extinction pressures effectively and make informed conservation recommendations. Future conservation efforts should be targeted towards ensuring remnant habitat patches in agricultural areas are retained, rather than investing in campaigns to mitigate illegal persecution which seems to only occur rarely.

Key-words: Agriculture, camera-trap surveys, conservation, habitat fragmentation, habitat loss, human persecution, *Leopardus guigna*, occupancy dynamics, random response technique, illegal killing.

Introduction

Land-use change is one of the greatest threats facing terrestrial biodiversity globally (Sala *et al.* 2000). Long-term species persistence is being negatively influenced by habitat loss, fragmentation, degradation and isolation (Henle *et al.* 2004b). The impacts of these land-use change processes include, for example, declines in habitat specialist population sizes (Bender, Contreras & Fahrig 1998), decreased reproductive rates due to edge effects (Lahti 2001), increased inter-specific competition between habitat specialists and generalists (Marvier, Kareiva & Neubert 2004) and reduced genetic variation (Napolitano *et al.* 2015a). In general, species with traits such as a low reproductive rate, low population density, large individual area requirements or a narrow niche are more sensitive to habitat loss and fragmentation (Fahrig 2002; Henle *et al.* 2004a) and, therefore, have a higher risk of extinction (Purvis *et al.* 2000). Consequently, many territorial carnivores are particularly vulnerable to habitat modification as a result of land-use change.

Additionally, in human-dominated landscapes, mammal populations are threatened directly by the behaviour of people (Ceballos *et al.* 2005). For instance, larger species (i.e. mammals with a body mass >1 kg) are often persecuted because they are considered a pest, food source or marketable commodity that can be traded (Woodroffe, Thirgood & Rabinowitz 2005). Carnivores are particularly vulnerable to retributive killing by people, normally in response to livestock predation or attacks on humans, presenting a highly complex management challenge for species of conservation concern

(Treves & Karanth 2003; Inskip & Zimmermann 2009). Indirectly, many mammals are also threated by factors such as the introduction of invasive plant species, which reduce habitat complexity (Rojas *et al.* 2011), or domestic pets, which can transmit diseases or compete for resources (Hughes & Macdonald 2013).

Increasingly in the future, carnivore conservation will require the application of novel initiatives outside of protected areas (Di Minin *et al.* 2016). To mitigate the threats they face in human-dominated landscapes effectively, through targeted conservation interventions, practitioners and policy-makers need to understand the relative contribution that issues such as habitat loss/fragmentation and persecution play in species population declines. This necessitates an integrated and interdisciplinary research approach (Clark *et al.* 2001). First of all, it is important to determine the differentiated impacts of habitat loss and fragmentation on a species, as the conservation actions required to alleviate the pressures associated with the two processes are likely to be different (Fahrig 2003; Fischer & Lindenmayer 2007). For instance, if habitat loss is the key driver, then large patches may need to be protected to ensure long-term survival, whereas a certain configuration of remnant vegetation may be imperative if fragmentation is the main threat. Secondly, it is important to understand if, how and why people persecute species of conservation concern (St John, Keane & Milner-Gulland 2013). Studies which examine human wildlife 'conflict' tend to focus on understanding: (i) patterns of livestock predation (e.g. Treves *et al.* 2004); (ii) motivations and attitudes towards wildlife via in-depth qualitative methods (e.g. Inskip *et al.* 2014); or, (iii) ways that humans can co-exist with carnivores (Sillero-Zubiri & Laurenson 2001; Treves *et al.* 2006). However, despite this valuable body of work, there seems to be a paucity of interdisciplinary research that evaluates explicitly both ecological and social drivers of species decline in a single coherent quantitative framework, across geographic scales pertinent to informing conservation decision-making (Dickman 2010).

Here we consider how threats to carnivores may be assessed across a human-dominated landscape, using the guiña (*Leopardus guigna*), an International Union for Conservation of Nature (IUCN) Red

Listed felid, as a model species. Specifically, we examine how habitat loss, fragmentation and human pressures may interact and impact upon this mammal, using data derived from camera-trap surveys, remote-sensed images and household questionnaires. These factors are integrated and evaluated within multi-season occupancy dynamics models. We argue that by combining ecological and social data, we can ultimately provide a more robust evidence-base for informing conservation efforts.

Methods

Study system

The study was conducted in the Araucanía region in southern Chile, at the northern limit of the South American temperate forest eco-region (39º15´S, 71º48´W) (Armesto *et al.* 1998). The system comprises two distinct geographical sections common throughout Southern Chile: the Andes mountain range and central valley. Land-use in the latter is primarily intensive agriculture (e.g. cereals, livestock, fruit trees) and urban settlements, whereas farmland in the Andes (occurring <600 m.a.s.l) is less intensively used and surrounded by tracks of continuous forest on steep slopes and protected areas (>800 m.a.s.l; Fig. 1). The natural vegetation across the study region consists of deciduous and evergreen Nothofagus forest (Luebert & Pliscoff 2006), which remains as a patchy mosaic in agricultural valleys and as continuous tracts at higher elevations within the mountains (Miranda *et al.* 2015).

The guiña is the smallest neotropical felid (<2 kg) and is categorised as Vulnerable by the IUCN (Napolitano *et al.* 2015b). It is thought to require forest habitat with dense understory and the presence of bamboo (*Chusquea* spp.) (Nowell & Jackson 1996; Dunstone *et al.* 2002), but is also known to occupy remnant forest patches within agricultural areas (Sanderson, Sunquist & W. Iriarte 2002; Acosta-Jamett & Simonetti 2004; Gálvez *et al.* 2013; Fleschutz *et al.* 2016). Guiñas are considered pests by some people as it can predate chickens and, while the extent of persecution has not been formally assessed, retributive killings have been reported (Sanderson, Sunquist & W. Iriarte 2002; Gálvez *et al.* 2013). Retributive killing predominately occurs when the felid enters chicken coups (Gálvez & Bonacic 2008). Due to these attributes, the species makes an ideal case study to

137 explore how habitat loss, fragmentation and human pressures may combine to influence occupancy
138 dynamics of a territorial carnivorous mammal in a human-dominated landscape.
139
140 ***Data collection***
141 *Carnivore occupancy camera-trap survey*
142 To ascertain and quantify the processes driving occupancy dynamics of the species, characterised as
143 the probability of a sample unit (SU) becoming occupied (local colonisation) or unoccupied (local
144 extinction), we conducted a camera-trap survey. Potential SUs were defined by laying a grid of 4 km^2
145 across the study region, representing a gradient of forest habitat fragmentation due to agricultural use
146 and human settlement below 600 m.a.s.l. The size of the SUs was informed by mean observed guiña
147 home range size estimates of collared individuals in the study area (MCP 95% mean=270 ±137 ha;
148 Schüttler et al. unpublished data).
149
150 We used a flexible occupancy-modelling framework that can account for imperfect detection and
151 missing observations (MacKenzie *et al.* 2003). In this study system, detectability was modelled based
152 on the assumption that a two-day survey block is a separate independent sampling occasion. This time
153 threshold was chosen because individuals do not stay longer than this time in any single location
154 (Schüttler et al. unpublished data). Minimum survey effort requirements (number of SUs and
155 sampling occasions) were determined following Guillera-Arroita, Ridout & Morgan (2010) using
156 species specific parameter values from Gálvez *et al.* (2013) and a target statistical precision in
157 occupancy estimation of SE<0.075. A total of 145 SUs were selected at random from the grid of 230,
158 with 73 and 72 located in the central valley and Andes mountain valley respectively (Fig. 1). The
159 Andean valleys were surveyed for four seasons (summer 2012, summer 2013, spring 2013, summer
160 2014), while the central valley was surveyed for three (the latter three seasons). A total of four
161 rotations (i.e. blocks of camera-traps) were used to survey all SUs within a 100 day period each
162 season. Detection and non-detection data were thus collected for 20-24 days per SU, resulting in 10-
163 12 sampling occasions per SU. Two camera-traps (Bushnell ™trophy cam 2012) were used per SU,
164 positioned 100-700 m apart, with a minimum distance of >2 km between camera-traps in adjacent

SUs. The detection histories of both camera-traps in a SU were pooled, and camera-trap malfunctions or thefts were treated as missing observations.

Habitat loss/fragmentation predictors of occupancy dynamics

The extent of habitat loss and fragmentation were evaluated using biologically meaningful metrics which have been reported in the literature as being relevant to guiña, using either field or remote-sensed landcover data (Table 1 and Appendix S1 & Table S1 in Supporting Information). The metrics were measured within a 300 ha circular buffer, centred on the midpoint between both cameras in each SU, using FRAGSTATS 4.1 (McGarigal *et al.* 2002).

Microhabitat predictors of detection probability

The microhabitat surrounding a camera-trap might influence species activity (Acosta-Jamett, Simonetti, 2004), and was therefore surveyed within a 25 m radius around each camera-trap, as this is deemed to be the area over which localised conditions may influence species detectability (Table S1). The data from both camera-traps in each SU were pooled and median value was used.

Human encounter/pressure predictors of occupancy dynamics

We administered a questionnaire (Appendix S2) face-to-face with residents living in the one or two households closest to the camera-traps within each SU, from May to September 2013. The aim was to solicit information from people living in the study region regarding their socio-demographic/economic background, guiña encounters, extent of livestock predation by guiña, tolerance to hypothetical livestock predation, ownership of dogs on the land parcel and whether they had ever killed a guiña. As it is illegal to kill a guiña in Chile (Law 19.473 Ministry of Agriculture), the Randomized Response Technique (RRT) method was used to ask this sensitive question. Questionnaires were administered by NG who is Chilean and has lived in the study region for over 10 years. The questionnaire was piloted with 10 local householders living outside the SUs and their feedback was used to improve the wording, order and time scale of predation and encounter questions.

The potential occupancy model predictors (Table 1 and Appendix S2 & Table S1) were calculated per SU. Where householder questionnaire responses were categorically different (i.e. one household report predation and the other did not) presence of the behaviour was recorded. For all quantitative measures, median values were used.

Predicting killing prevalence across the study region

We estimated the prevalence of guiña killing across the study region via analysis of the RRT data. A total of 1000 bootstraps were conducted to obtain a 95% confidence interval. We tested predictors of killing behaviour, such as socio-economic background, knowledge of protection status, frequency of guiña encounters, predation levels and tolerance to hypothetical predation (Appendix S2). We used R (version 3.2.3; R Core Team, 2014) to run the RRlog function of the package RRreg (version 0.5.0; Heck & Moshagen 2016) to conduct a multivariate logistic regression using the model for 'forced response' RRT data. We fitted a logistic regression model with the potential predictors of killing behaviour and evaluated their significance with likelihood ratio tests (LRT ΔG^2).

Multi-season occupancy modelling and selection procedure

We fitted models of occupancy dynamics (MacKenzie *et al.* 2003) using PRESENCE, which obtains maximum-likelihood estimates via numerical optimisation (Hines 2006). The probabilities of occupancy (ψ), colonisation (γ), local extinction (ε) and detection sites (p) were used as model parameters. Model residuals of detection/non-detection data for each season were tested for the existence of spatial autocorrelation using Moran's *I* (Dormann *et al.* 2007). We used a fixed band of 3 km from the midpoint of cameras, equating to an area three times larger than the home range of the guiña.

We conducted a preliminary investigation to assess whether a base model structure with Markovian dependence was more appropriate for describing seasonal dynamics, rather than assuming no occupancy changes occur or that changes happen at random (MacKenzie *et al.* 2006). Once the best model structure had been determined, we then fitted models with habitat loss/fragmentation, human

encounter/pressure and microhabitat predictors. A total of 15 potential model predictors were tested for collinearity and, in instances where variables were correlated (Pearson's or Spearman's $|r|>0.7$), we retained the covariate that conferred greater ecological/social meaning and ease of interpretation. All continuous variables, except percentages, were standardized to z-scores. We approached model selection by increasing model complexity gradually (Table 3), fitting predictors for each model parameter separately and assessing model performance using Akaike's Information Criterion (AIC). Models that were within <2 ΔAIC were considered to have substantial support (Burnham & Anderson 2002), and thus these predictors were selected and used in the next step in a forward manner (e.g. Kéry, Guillera-Arroita & Lahoz-Monfort 2013). To prevent over fitting the models (Burnham & Anderson 2002) we kept those with only one predictor per parameter, with the exception of one model which evaluated the additive effect of shrub and forest cover (shrub is a marginal habitat for the case study species; Dunstone *et al.* 2002).

A set of *p* models were fitted using the best base structure. Subsequently, we evaluated models that included habitat loss/fragmentation and human encounter/pressure effects on ψ_1, while keeping γ and ε season specific. The best ψ_1 and *p* models were then used to add further complexity to the γ and ε components. For ε we fitted all predictors. However, we assume that γ is only influenced by habitat loss/fragmentation predictors, not human encounter/pressure. To explore the candidate model space, we worked on the structure for ε followed by γ, and then repeated the process vice versa, following Kéry et al. (2013). A constant or null model was included in all candidate model sets. Models with convergence problems or implausible parameter estimates were eliminated from each set.

To evaluate goodness of fit of the final model, we tested an additive model with top ranked predictors, for ε or γ, if they presented sufficient support (>4 AIC units) from other models. Goodness of fit was evaluated with the MacKenzie and Bailey parametric bootstrap test (5000 iterations) for dynamic occupancy models, which provides a model fit statistic for all seasons (*P*-Global) and per season, in the R package "AICcmodavg". We used the *predict* function in R package "unmarked" (Fiske &

Chandler 2011) to produce plots of estimated relationships with the predictors and to derive estimates of occupancy for each of the seasons.

Results

Habitat loss/fragmentation predictors of occupancy dynamics

We excluded four habitat loss/fragmentation predictors due to collinearity with extent of forest cover and number of patches (Tables 1 & S1). Across the study region, variation in the degree of habitat loss and fragmentation was substantial. Extent of forest cover in SU's ranged from 1.8% to 76% (mean=27.5%; SD=18.9), and shrub cover followed a similar pattern (range: 9.1% to 53.1%; mean=26%; SD=8.3%). The number of habitat patches per SU varied between 14 and 163 (mean=52.9; SD=25.7), and patch shape was diverse (index ranging 1.3 (highly irregular forms) - 7.8 (regular forms); mean=3.13; SD=1.3). Some SUs include a relatively high length of edge with 48,405 m, whereas others had as little as 4,755 m.

Human encounter/pressure predictors of occupancy dynamics and killing prevalence

A total of 233 respondents completed the questionnaire. The majority (i.e. >50%) were between 46 and 67 years old and had lived in their property for 25 to 50 years. Properties were 1-1,200 ha in size, with a median of 29 ha. Land subdivision within SUs also varied widely from 1 to 314 properties (mean=41.3; SD=37.2). Respondents, on average, received a monthly income equivalent to US$ 558 (SE= 2.81) and had received 10 years of formal schooling.

Encounters with the guiña were sparse. Nearly half of the respondents (49%, n=116) reported seeing a guiña during their lifetime. On average, the sighting occurred 17 years ago (SD=15). However, in the last 4 and 10 years, only 10% and 21% of people respectively had encountered the case study species. Predation events were also uncommon. Only 16% of respondents (n=37) attributed a livestock predation event in their lifetime to the guiña, with just 7% (n=16) reporting that this had occurred in the past decade. Of guiña predation events in the last 10 years, 81% (n=13) were recorded in Andean SUs. The number of people with an intent to kill the case study species was greater than those who

had encountered it or suffered a livestock predation event; 38% (n=89) of respondents stated that they would kill a guiña if two chickens were predated, increasing to 60% (n=140) if 25 chickens were predated. Using the RRT method, we found that the proportion of respondents who had killed a guiña was 0.09 (SE=0.08; 95% CI=0.02-0.16). The likelihood of a respondent having killed an individual significantly increased when they depended on their land parcel for economic livelihood (β=4.14, SE=3.35; LRT ΔG^2 =5.80, p=0.01) and had had more frequent encounters with the species (β=5.37, SE=4.01; LRT ΔG^2 =8.57, p<0.00).

Occupancy dynamics

A total of 23,373 camera-trap days returned 713 sampling occasions with guiña detections (season 1=96; season 2=185; season 3=240; season 4=192). The naïve occupancy estimate (i.e. proportion of sites with detection) was similar across all four seasons (0.54; 0.52; 0.58; 0.59) and between the central valley and Andean SUs (both areas >0.5). No spatial autocorrelation was observed among SUs during any survey season, thus a correction parameter was not needed (season 1 Moran's I=-0.03 (α=0.74); season 2 I=0.05 (α=0.31); season 3 I=0.05 (α=0.36); season 4 I=0.07 (α=0.17)).

Our preliminary evaluation indicated that the Markovian dependence base model structure was the most appropriate, meaning that site occupancy in any given season is dependent on the occupancy status from the previous season (Table 2). Model 1.1 was chosen as the base structure for the modelling procedure, with ψ_1 representing occupancy status of sites in the first season. It was selected because: (i) it is supported by AIC; and, (ii) its parameterisation using ε and γ allowed the role of different predictors to be tested.

Model selection for p (models 2.1-2.7; Table 3) revealed a positive relationship with understory vegetation cover (β_1 0.343; SE=0.055). There was no evidence of an effect associated with the rotational survey design and none of the other predictors were substantiated by the model selection. Forest cover best explained ψ_1 (models 3.0-3.6; Table 3), with initial occupancy higher in sites with less forest cover, although the parameter estimate was small (β_1 =-0.0363; SE=0.0138). Adding shrub

304 cover only improved model fit marginally. Fragmentation metrics and land subdivision were not
305 supported as good predictors.
306
307 Model selection for ε and γ (models 4.0-4.18 and 5.0-5.12; Table 3) reflected the same trends,
308 irrespective of the order in which parameters were considered. Extinction, rather than γ, yielded
309 predictors that improved model fit compared to the null model. Where predictors were fitted first on γ
310 (models 5.0-5.5), none of the models tested improved fit substantially compared to the null model.
311 This indicated that, of the available predictors, γ was only explained by seasonal differences. Human
312 encounter/pressure predictors, such as experience of livestock predation or intention to kill, were not
313 supported as drivers of either ψ_1 or ε (Table 3).
314
315 We fitted a final model (5.6) from predictors identified in the two top competing ε models (5.7 and
316 5.8), number of patches and land subdivision, which were >5 AIC units better than the next models.
317 The model with both covariates showed higher support (Table 3; ID 5.6). The goodness-of-fit test run
318 on the final model (ID 5.6) suggested lack of fit based on the global metric (*P*-global<0.05), but
319 inspection of survey-specific results show no such evidence of lack of fit for any of the seasons
320 (p>0.05) apart from season 2 (p=0.032). Inspecting the season 2 data, we find that the relatively large
321 chi-square statistic value appears to be driven by just a few sites with unlikely capture histories
322 according to the model (i.e. <12). Given this, and the fact that data from the other seasons do not show
323 lack of fit, we deem that the final model explains the data appropriately. Estimates suggest that
324 increasing the number of habitat patches, and decreasing land subdivision will reduce extinction
325 probability (β_1 =-0.900; SE=0.451 and β_1 =0.944; SE=0.373 respectively; Fig. 2). Occupancy
326 estimates were high across seasons with derived seasonal estimates of 0.78 (SE=0.09), 0.64
327 (SE=0.06), 0.80 (SE=0.06) and 0.83 (SE=0.06).
328
329 **Discussion**
330 The guiña is an elusive forest specialist. As such, one might predict that the species would be highly
331 susceptible to both habitat loss and fragmentation (Henle *et al.* 2004a; Ewers & Didham 2006). While

332 the relationship between occupancy and higher levels of forest cover (Fig. 2) does suggest that guiña
333 are likely to occupy areas with a large spatial extent of available habitat, our results also indicate that
334 the species can tolerate extensive habitat loss. Indeed, the findings highlight that intensive agricultural
335 landscapes are relevant for conservation of guiña and should not be dismissed as unsuitable. Spatially,
336 the processes driving the occupancy dynamics of this carnivore are affected by fragmentation and
337 human pressure through land subdivision. Ensuring that plenty of remnant habitat patches are retained
338 in the landscape, and land subdivision is reduced so that existing bigger farms are preserved, could
339 ultimately safeguard the long-term survival of this threatened species, rather than focusing merely on
340 the real extent of habitat.
341
342 Although previous studies have suggested that human persecution may be a factor contributing to the
343 decline of the guiña (Nowell & Jackson 1996; Sanderson, Sunquist & W. Iriarte 2002), illegal killing
344 in the study region appears low. Despite the fact that the species occupies a large proportion of the
345 landscape across seasons, people only report encountering the carnivore, or suffering poultry
346 predation rarely. This elusive behaviour is further reflected and reinforced by our low camera-trap
347 detection probability (p<0.2). Twenty-one respondents (9%) admitted to killing a guiña over the last
348 decade yet we do not know the quantity of cats killed (i.e. not measured in this study). Identification
349 of individual cats from camera-trap images is unfeasible (F. Blair unpublished data), meaning that it is
350 not currently possible to estimate changes in abundance through time or conduct population viability
351 analyses. Consequently, we are unable to determine whether this prevalence of illegal killing is
352 having a detrimental impact on the population size of the species. However, there is genetic evidence
353 that guiña populations have suffered significant population reductions in the recent past (Napolitano *et*
354 *al.* 2014). Where available evidence suggests that illegal killing might be having an adverse impact on
355 populations, conservation interventions to reduce persecution should be of benefit to carnivores,
356 particularly measures which prevent females from being targeted (Chapron *et al.* 2008).
357
358 Following farming trends globally, larger properties in the agricultural areas of southern Chile are
359 generally associated with high intensity production, whereas smaller farms are mainly subsistence-

360 based systems (Carmona *et al.* 2010). It is therefore interesting, but perhaps counterintuitive, that we
361 found occupancy to be higher (lower local extinction) where there is less land subdivision. It is likely
362 that a greater number of small farms will increase human persecution as a result of higher human
363 density (Woodroffe 2000). Also, higher subdivision imposes pressure on natural resources, due to
364 more households being present in the landscape (e.g. Liu *et al.* 2003), which has been shown to
365 reduce the quality of remaining habitat patches as a result of frequent timber extraction, livestock
366 grazing (Carmona *et al.* 2010) and competition/interference by domestic animals and pets (Sepúlveda
367 *et al.* 2014). Native vegetation in non-productive areas, including ravines or undrainable soils with a
368 high water table, is normally spared within agricultural areas (Miranda *et al.* 2015), and these patches
369 of remnant forest could provide adequate refuge, food resources and suitable conditions for carnivore
370 reproduction (e.g. Schadt *et al.* 2002). Additionally, another factor driving the subdivision of land and
371 degradation of remnant forest patches across agricultural areas is the growing demand for residential
372 properties (Petitpas 2010). This is facilitated by Chilean law, which permits agricultural land to be
373 subdivided to a minimum plot size of 0.5 ha. Furthermore, it is common practice for sellers and
374 buyers to completely eliminate all understory vegetation from such plots (C. Rios, personal
375 communication) which, as demonstrated by detection being higher in dense understory, is a key
376 component of habitat quality.
377
378 Our results suggest that land subdivision, and the associated processes outlined above, are likely to be
379 the main threat to guiña in the study region. Conservationists should thus engage with householders,
380 land-use planners and developers proactively to advocate actions, such as protection of remnant
381 habitat patches in the landscape from livestock entrance, which will improve understory cover and
382 quality. Regulatory guidelines and enforcement may also be required (e.g. Hansen *et al.* 2005). For
383 example, government agencies may need to subsidise farmers to fence off some of forested areas on
384 their land. Conservation measures such as these should prove to be more effective than investing
385 limited conservation resources on retributive killing mitigation, except in areas where reported
386 encounters with the felid might be high.
387

Our case study highlights the value of using multi-season modelling techniques to evaluate and differentiate between the effects of habitat loss and fragmentation by not only contrasting these processes with initial occupancy, but also with factors that explain changes in status (i.e. extinction, colonisation), all corrected for imperfect detection of an elusive species. For the guiña, which do not appear to be impacted heavily by habitat loss, potentially because they are relatively mobile, it is habitat configuration (i.e. patterns of fragmentation) and human pressure that drive dynamics across the landscape. Indeed, our findings imply that these remnant patches play a key role in supporting this carnivore in areas where there has been substantial habitat loss and, perhaps, might even offset local extinctions associated with habitat cover (Fahrig 2002). However, areas with high land subdivision and a large number of patches could be acting as ecological traps if source-sink dynamics are operating in the landscape (Robertson & Hutto 2006). Another issue to be aware of is that the effects of habitat loss/fragmentation could be confounded by time, and it is possible that we are not yet observing the impacts of habitat loss (Ewers & Didham 2006). However, this is unlikely to be the case in this study system as over 67% of the original forest cover was lost by 1970 and, since then, deforestation rates have been low (Miranda *et al.* 2015).

The research presented here demonstrates the benefits of integrating ecological and social data into a single modelling framework to gain a more systematic understanding of the drivers of species decline in a human-dominated landscape. It has allowed us to tease apart the relative importance of different threats to a carnivore and make informed recommendations as to the type of conservation efforts that should be prioritised.

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572 **Figure Legends**

573

574 **Figure 1:** Distribution of landcover classes and protected areas across the study region in southern
575 Chile, including the forest habitat of our case study species, the guiña (*Leopardus guigna*). The two
576 zones within which the 145 sample units (SU: 4 km2) were located are indicated, with 73 SUs in the
577 central valley (left polygon) and 72 within the Andes (right polygon). The positions of each SU are
578 not shown, complying with the ethics guidelines associated with studying illegal human behaviour.
579 Illustrative examples of the variation in landscape configuration within SUs across the human-
580 domination gradient are provided (bottom of image).

581

582 **Figure 2** Predicted effects of forest cover, understory density, number of habitat patches and land
583 subdivision on multi-season occupancy model parameters for the guiña (*Leopardus guigna*). These
584 results correspond to the final selected model [ψ_1(Forest), *p*(season+Understory),
585 ε(season+PatchNo+Subdivision), γ(season)]. Grey lines delimit 95% confidence intervals.

586

587 **Table 1:** Habitat loss/fragmentation, human encounter\pressure and microhabitat predictors evaluated
588 when modelling occupancy (ψ), colonisation (γ), extinction (ε) and detection (*p*) probability
589 parameters of multi-season camera-trap surveys of guiña (*Leopardus guigna*). Further details can be
590 found in Appendix S1, S2 and Table S1 in the Supporting Information.
591

Parameter	Predictor	Abbreviation in models
	Habitat loss/fragmentation	
ψ, ε, γ	Percent of forest cover/habitat[†]	Forest
ψ, ε, γ	Percent shrub cover/marginal habitat	Shrub
ψ, ε, γ	Number of forest patches	PatchNo
ψ, ε, γ	Shape index forest patches	PatchShape
ψ, ε, γ	Forest patch size area[‡]	PatchAreaW
ψ, ε, γ	Forest patch continuity[‡]	Gyration
ψ, ε, γ	Edge length of forest land cover class	Edge
ψ, ε, γ	Landscape shape index of forest[§]	LSI
ψ, ε, γ	Patch cohesion[‡]	COH
	Human encounter/pressures	
ψ, ε	Land subdivision	Subdivision
ψ, ε	Intent to kill	Intent
ψ, ε	Predation	Predation
ψ, ε	Frequency of predation	FQPredation
ψ, ε, *p*	Frequency of encounter[††]	FQEncounter
ψ, ε	Number of dogs	Dogs
	Microhabitat	
p	Bamboo density (*Chusquea* spp.)	Bamboo
p	Density of understory	Understory
p	Sample Unit rotation block	Rotation
p	Intensity of livestock activity	Livestock
p	Intensity of logging activity	Logging
p	Water availability	Water

592 [†]Pools together all forest types: old-growth, secondary growth, and wetland forest
593 [‡] Predictor excluded due to collinearity with percent of forest cover (Pearson's $|r|>0.7$)
594 [§] Predictor excluded due to collinearity with number of forest patches (Pearson's $|r|>0.7$)
595 [††] Predictor also fitted with detection probability
596
597

598 **Table 2:** Seasonal occupancy dynamics models for territorial species following Mackenzie et. al.
599 (2006), applied to the guiña (*Leopardus guigna*), to define the base model structure for the subsequent
600 model selection procedure to evaluate habitat loss/fragmentation, microhabitat and human
601 encounter/pressure covariates. Fitted probability parameters are occupancy (ψ), colonisation (γ),
602 extinction (ε) and detection (p). Models assess whether changes in ψ do not occur (ID 1.6), occur at
603 random (ID 1.5, 1.4) or follow a Markov Chain process (i.e. site occupancy status in a season is
604 dependent on the previous season) (ID 1.0, 1.1, 1.2, 1.3). ψ_1 refers to ψ in the first of four seasons
605 over which the guiña was surveyed. Model selection procedure is based on Akaike's Information
606 Criterion (AIC). ΔAIC is the difference in AIC benchmarked against the best model, w_i is the model
607 weight, K the number of parameters, and -2*loglike is the value of the log likelihood at its maximum.
608 The selected model is highlighted in bold.
609

ID	Seasonal dynamic models	ΔAIC	w_i	K	-2*loglike
1.0	ψ(.), γ(.), {$\varepsilon = \gamma(1-\psi)/\psi$}, p(season)	0.00	0.443	6	3982.93
1.1	**ψ_1(.), ε(season), γ(season), p(season)**	**0.36**	**0.370**	**11**	**3973.29**
1.2	ψ_1(.), ε(.), γ(.), p(season)	1.88	0.173	7	3982.81
1.3	ψ_1(.), ε(.), γ(.), p(.)	6.83	0.015	4	3993.76
1.4	ψ_1(.), γ(.),{$\varepsilon = 1-\gamma$}, p(season)	41.78	0.000	6	4024.71
1.5	ψ_1(.), γ(season),{$\varepsilon = 1-\gamma$}, p(season)	42.78	0.000	8	4021.71
1.6	ψ(.), {$\gamma = \varepsilon = 0$}, p(season)	104.11	0.000	6	4087.04

610
611

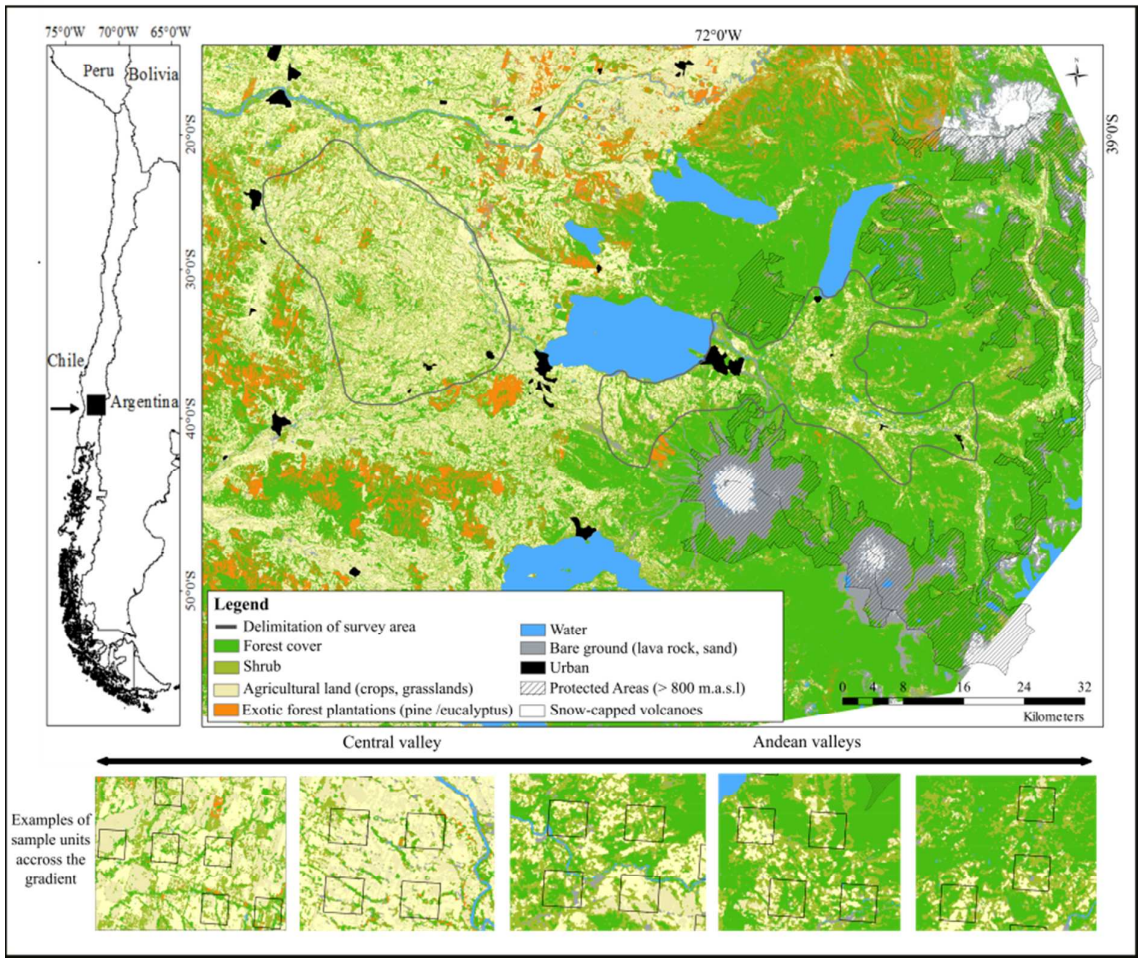
612 **Table 3:** Multi-season models of initial occupancy (ψ_1), extinction (ε), colonisation (γ) and detection
613 (p) probability with habitat loss/fragmentation, microhabitat and human encounter/pressure covariates
614 for guiña (*Leopardus guigna*). Covariates were evaluated with a base model of seasonal dynamics
615 [ψ_1(.), ε(season), γ(season), p(season)] using a step-forward model selection procedure and Akaike's
616 Information Criterion (AIC). ψ_1 refers to ψ in the first of four seasons over which the guiña was
617 surveyed, with occupancy dynamics following a Markov Chain process. ΔAIC is the difference in
618 AIC benchmarked against the best model, w_i is the model weight, K the number of parameters, and -
619 2*loglike is the value of the log likelihood at its maximum. The selected models for each parameter
620 are highlighted in bold and used in the next step. ε was fitted first followed by γ, then vice versa.

ID	Fitted parameter	ΔAIC	w_i	K	-2*loglike
	Detection/fitted with ψ_1(.), ε(season), γ(season)				
2.0	***p*(season+Understory)**	**0.00**	**0.9999**	**12**	**3934.47**
2.1	*p*(season+Bamboo)	18.48	0.0001	12	3952.95
	Initial occupancy/fitted with ε(season), γ(season), p(season+Understory)				
3.0	**ψ_1(Forest)**	**0.00**	**0.5425**	**13**	**3927.46**
3.1	ψ_1(Forest+Shrub)	1.24	0.2918	14	3926.7
3.4	ψ_1(PatchNo)	4.00	0.0734	13	3931.46
3.5	ψ_1(.)	5.01	0.0443	12	3934.47
3.6	ψ_1(Subdivision)	5.69	0.0315	13	3933.15
3.7	ψ_1(Dogs)	7.00	0.0164	13	3934.46
	Extinction first/fitted with ψ_1(Forest), p(season+Understory)				
4.0	**ε(season+PatchNo), γ(season)**	**0.00**	**0.4692**	**14**	**3920.10**
4.1	**ε(season+Subdivision), γ(season)**	**0.36**	**0.3919**	**14**	**3920.46**
4.2	ε(season+PatchShape), γ(season)	5.15	0.0357	14	3925.25
4.3	ε(season+Predation), γ(season)	5.24	0.0342	14	3925.34
4.4	ε(season), γ(season)	5.36	0.0322	13	3927.46
4.5	ε(season+FQencounter), γ(season)	5.92	0.0243	14	3926.02
4.6	ε(season+FQPredation), γ(season)	7.24	0.0126	14	3927.34
	Colonisation second/fitted with ψ_1(Forest), p(season+Understory)				

4.7	**ε(season+PatchNo), γ(season)**	**0.00**	**0.1877**	**14**	**3920.10**
4.8	**ε(season+Subdivision), γ(season)**	**0.36**	**0.1568**	**14**	**3920.46**
4.9	ε(season+Subdivision), γ(season+PatchShape)	0.79	0.1265	15	3918.89
4.10	ε(season+PatchNo), γ(season+PatchShape)	1.29	0.0985	15	3919.39
4.11	ε(season+Subdivision), γ(season+PatchNo)	1.63	0.0831	15	3919.73
4.12	ε(season+PatchNo), γ(season+Edge)	1.84	0.0748	15	3919.94
4.13	ε(season+PatchNo), γ(season+Forest)	1.98	0.0698	15	3920.08
4.14	ε(season+Subdivision), γ(season+Edge)	2.16	0.0638	15	3920.26
4.15	ε(season+ Subdivision), γ(season+Forest)	2.20	0.0625	15	3920.30
4.16	ε(season+Subdivision), γ(season+Forest+Shrub)	3.50	0.0326	16	3919.60
4.17	ε(season+PatchNo), γ(season+Forest+Shrub)	3.60	0.0310	16	3919.70
4.18	ε(season), γ(season)	5.36	0.0129	13	3927.46
	Colonisation first/fitted with ψ_1(Forest), p(season+Understory)				
5.0	**ε(season), γ(season)**	**0.00**	**0.3303**	**13**	**3927.46**
5.1	ε(season), γ(season+PatchShape)	0.96	0.2044	14	3926.42
5.2	ε(season), γ(season+PatchNo)	1.55	0.1522	14	3927.01
5.3	ε(season), γ(season+Edge)	1.89	0.1284	14	3927.35
5.4	ε(season), γ(season+Forest)	1.95	0.1246	14	3927.41
5.5	ε(season), γ(season+Forest+Shrub)	3.41	0.06	15	3926.87
	Extinction second/fitted with ψ_1(Forest), p(season+Understory)				
5.6	**ε(season+PatchNo+Subdivision), γ(season)**	**0.00**	**0.8275**	**15**	**3913.45**
5.7	ε(season+PatchNo), γ(season)	4.65	0.0809	14	3920.10
5.8	ε(season+Subdivision), γ(season)	5.01	0.0676	14	3920.46
5.9	ε(season+PatchShape), γ(season)	9.80	0.0062	14	3925.25
5.10	ε(season+Predation), γ(season)	9.89	0.0059	14	3925.34
5.11	ε(season), γ(season)	10.01	0.0055	13	3927.46
5.12	ε(season+FQEncounters), γ(season)	10.57	0.0042	14	3926.02
5.13	ε(season+FQPredation), γ(season)	11.89	0.0022	14	3927.34

621

622 **Figure 1**



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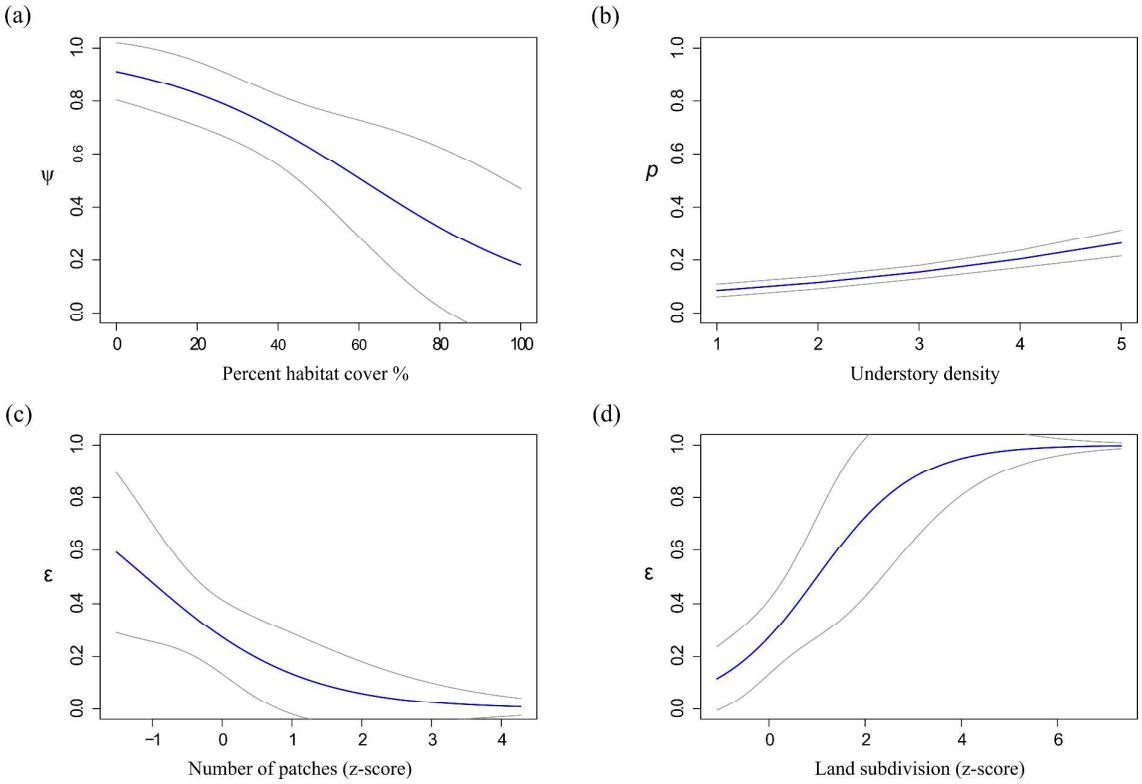
633 **Figure 2**



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636 # Supporting Information

637

638 **Appendix S1: Landcover classification of study area**

639 Landcover classification was carried out using a composite of four Aster images at 15 m resolution
640 from between 2002 and 2007. Native forest cover within the study region did not change significantly
641 between 1983 and 2007 (Petitpas 2010; Miranda *et al.* 2015). In addition, the current extent and
642 configuration of forest across the sample units (SUs) has not altered perceptibly when compared
643 visually with up-to-date Google Earth imagery from 2014. The study region was categorised into nine
644 landcover classes ((i) water; (ii) forest, (iii) forest regrowth, (iv) shrub/bog, (v) grassland, (vi) hualve
645 (inundated forests), (vii) plantation, (viii) crop/pasture/orchard and (ix) bare ground/sand/lava rock)
646 using a supervised classification with maximum likelihood estimation, based on field data from 738
647 training points. A further 738 points were used to verify classification accuracy, which was 'almost
648 perfect' (Kappa= 0.81 (SE= 0.017); Landis & Koch 1977; Congalton 1991). Urban landcover
649 digitised by hand and added as a tenth class. Image processing and classification were conducted in
650 ERDAS Imagine 2014 (Hexagon Geospatial, Norcross, GA, USA) and ArcMap v.10.1 (ESRI,
651 Redlands, CA, USA).

652

653

654 **Appendix S2: Generation of the human encounter/pressure predictors used to model multi-**
655 **season occupancy dynamics of guiña (*Leopardus guigna*)**

656 A translated version of the questionnaire can be requested from the corresponding author. The
657 questionnaire consisted of six sections. The first part included socio-demographic/economic questions
658 relating to age, amount of schooling, livelihood activities and income. The next section focussed on
659 questions regarding killing wild animals, including species with protected (e.g. puma/ guiña) and non-
660 protected status (e.g. introduced wild boar). To prevent any bias in responses, our questions included
661 all native carnivores known to occur across the study region, as well as free-roaming domestic dogs.
662 As killing of protected species is an illegal activity, we employed the Randomized Response
663 Technique (RRT) method described in St John et al. (2010). A dice was used as randomization tool;
664 respondents were asked to provide a truthful answer if they rolled a one, two, three or four, must
665 answer "yes" if they rolled a five (irrespective if it is true answer or not) and must answer "no" if the
666 dice landed on six. The time period used to provide context to the question was 'over the last ten
667 years', which was deemed most appropriate after the pilot exercise. Trial runs were conducted using
668 non-sensitive questions to ensure the RRT instructions were understood and being followed by the
669 respondents. Special care was taken to ensure that the interviewer could not see the number on the
670 rolled dice.
671
672 The third part of the questionnaire asked respondents to report livestock losses via predation over the
673 past year, or an alternative time period they could quantify. In the fourth section, participants were
674 probed about their knowledge of whether the hunting of each species was permitted or illegal, as well
675 as asking how frequently the species were encountered. A fifth section aimed to evaluate scenarios of
676 predation with a hypothetical livestock holding of 100 sheep and chickens. Respondents were asked
677 what behaviour they would display towards the carnivores occurring in the study region after a
678 specific level of predation (2, 10, 25, 50, >50 sheep or chickens) has been experience. For sheep
679 predation, we assessed the puma (*Puma concolor*) and domestic dogs (*Canis familiaris*), and for
680 chicken predation we asked about guiña and Harris hawk (*Parabuteo unicinctus*). In order not to bias
681 responses, respondents were offered a choice of possible actions (e.g. lethal controls, call authorities,

682 improve management, nothing, etc.). The final section centred on the management of livestock,
683 particularly sheep and chickens, in relation to behaviour such as enclosing livestock at night, the
684 distance of the closure from household, the number of domestic dogs/cats associated with the property
685 and how they are managed overnight (e.g. free-roaming, tethered), as well as how often they are fed
686 and the type of food they are given.
687
688

689 **Table S1:** Description of habitat loss/fragmentation, human encounter/pressure and microhabitat predictors used when modelling occupancy (ψ), colonisation
690 (γ), extinction (ε) and detection (*p*) probability parameters from multi-season camera-trap surveys of guiña (*Leopardus guigna*). Detailed description of
691 habitat loss/fragmentation metrics can be found in (McGarigal *et al.* 2002).

Predictor	Abbreviation in models	Description
Habitat loss/fragmentation		
Percent forest cover	Forest	Metric that measures habitat loss as the extent of forest cover in a sample unit (0-100). Forest cover was obtained by pooling old-growth and secondary forest landcover classes, which are both considered to be suitable guiña habitat (Nowell & Jackson 1996; Acosta-Jamett & Simonetti 2004).
Percent shrub cover	Shrub	Metric that measures the extent of shrub cover in a sample unit (0-100). The spatial configuration is not assessed because shrub is a marginal habitat and evaluated for an additive effect on forest cover. As shrub can be considered a marginal habitat for guiña (Dunstone *et al.* 2002; Sanderson, Sunquist & W. Iriarte 2002; Acosta-Jamett & Simonetti 2004), we also measured the extent of shrub cover to evaluate possible additive effects with habitat cover
Number of forest patches	PatchNo	Metric that measures the number of forest habitat patches (0-∞).
Shape index forest patches	PatchShape	Shape metric that measures the complexity of forest habitat patch shape compared to a square, weighted for the entire landscape. As the index value increases, that habitat patch shape is more irregular (1-∞).
Forest patch size area[†]	PatchAreaW	Metric that measures mean habitat patch area (0-∞) corrected for sample unit scale. It provides a landscape centric perspective of patch structure.
Forest patch continuity[†]	Gyration	Metric that measures habitat patch continuity (0-∞). It can be interpreted as the average distance an organism can move within the habitat before an edge is encountered (McGarigal *et al.* 2002). The value increases with greater habitat patch extent.
Edge length of forest	Edge	Area-edge metric that measures the total length (0-∞) of habitat patch edge across a sample unit. This can be used instead of edge density because we are comparing sample units of the same size (McGarigal *et al.* 2002). The value rises with increasing edge.
Landscape shape index of forest[‡]	LSI	Aggregation metric that compares the landscape level edge of the habitat to one without internal edges or a square (0-100). This is a measure of the level of fragmentation in a sample unit.
Patch Cohesion[†]	COH	Aggregation metric that measures the physical connectedness (0-1) of forest habitat cover by measuring the aggregation of patches.
Human encounter/pressures		

Land subdivision	Subdivision	Measures the number of land tenure divisions (i.e. owners) in a sample unit (0-∞). We expect higher subdivision to represent greater anthropogenic pressure and management variability from factors such as logging and presence of domestic dogs which were not measured directly in each sample unit (e.g. Theobald, Miller & Hobbs 1997; Hansen et al. 2005; Western, Groom & Worden 2009). Subdivision was based on the number of properties or land parcels recorded in each SU from national records (CIREN-CORFO, 1999).
Intent to kill	Intent	Intent to kill guiña by households in a sample unit (categorical: yes= 1, no= 0). This measure describes how a respondent states they would respond if a guiña two of their chickens. It is a highly conservative indicative measure of tolerance to livestock predation before lethal control is considered.
Predation	Predation	Occurrence of chicken predation by guiña in a sample unit (categorical: yes= 1, no= 0).
Frequency of predation	FQPredation	Frequency of chicken predation by guiña in a sample unit. Predation events were scaled to yearly frequency (0-∞).
Frequency of encounter[§]	FQEncounter	Numbers of encounters householders have had with guiña, scaled to a yearly frequency (0-∞). Frequency of encounters is also used to fit detection probability as a proxy for the elusiveness of the species.
Number of dogs	Dogs	Maximum number of free-roaming dogs, owned by the household, at night in proximity to the camera-traps (0-∞). We assume this value to be a conservative proxy to dog activity and an index of interference/competition by dogs. We also fitted extinction probability with free roaming dogs as they have been documented to interfere and kill wildlife in Chile (Silva-Rodriguez, Ortega-Solis & Jimenez 2010; Silva-Rodríguez & Sieving 2012), therefore we included average number of free roaming domestic dogs of nearby households (from our questionnaire Appendix S2 as a potential source of mortality. Because guiña are mainly nocturnal (Delibes-Mateos et al. 2014; Hernandez et al. 2015) we excluded households that restrain dogs at night.
Microhabitat[§]		
Bamboo density (*Chusquea* spp.)	Bamboo	Bamboo density (*Chusquea* spp.) within a 25 m radius of each camera-trap, recorded in five categorical percentage classes (Braun-Blanquet 1965).
Density of understory	Understory	Understory vegetation density within a 25 m radius of each camera-trap, recorded in five categorical percentage classes (Braun-Blanquet 1965).
SU rotation	Rotation	Each SU was included in one of four consecutively sampled rotations of camera-traps during each season.
Intensity of livestock activity	Livestock	Livestock activity next to each camera-trap visually assessed and recorded using three categories (high, medium or low intensity). Based on signs such as presence of animals, grazed vegetation, trampled paths and manure.
Intensity of logging activity	Logging	Logging activity next to each camera-trap visually assessed and recorded using three categories (high, medium or low intensity). Based on signs such as active firewood piles, clearings, logging paths, fresh stumps and fallen logs.
Water availability	Water	The availability of water was recorded as either present or absent at the patch level during each season (categorical: yes= 1, no= 0).

692 [†]Predictor excluded due to collinearity with percent of forest cover (Pearson's $|r|>0.7$)
693 [‡]Predictor excluded due to collinearity with number of forest patches (Pearson's $|r|>0.7$)
694 [§]Predictors fitted only with detection probability at the forest patch level

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